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Sara Labrousse

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Titre de la thèse

Beneath the sea ice: exploring elephant seal foraging strategy in Earth's extreme Antarctic polar environment

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devant le jury composé de

M.	Stéphane Blain	PR UPMC, LOMIC	*Président du jury*
M.	Christophe Barbraud	CR CNRS, CEBC	*Rapporteur*
M.	Ari Friedlaender	PR OSU, MMI	*Rapporteur*
M.	Christophe Guinet	DR CNRS, CEBC	*Examinateur*
M.	Jean-Baptiste Sallée	CR CNRS, LOCEAN	*Examinateur*
M.	Frédéric Bailleul	CR, SARDI	*Co-directeur de thèse*
M.	Mark Hindell	PR UTAS, IMAS	*Co-directeur de thèse*
M.	Jean-Benoit Charrassin	PR MNHN, LOCEAN	*Directeur de thèse*

"S'élancer à la conquête des terres vierges, c'est être poussé par le goût de l'aventure, par l'appétit scientifique ou encore par le mystérieux attrait de l'inconnu. Chacun de ces trois motifs eut sa part dans ma décision de repartir pour l'Antarctique"

Ernest Shackleton **Au coeur de l'Antarcticque : Vers le pôle Sud, 1908-1909**

Beneath the sea ice: exploring elephant seal foraging strategy in Earth's extreme Antarctic polar environment

Abstract: Understanding how physical properties of the environment underpin habitat selection of large marine vertebrates is crucial in identifying how and where animals acquire resources necessary for locomotion, growth and reproduction and ultimately their fitness. The Southern Ocean harbors one of the largest and most dynamic marine ecosystems on our planet which arises from the presence of two majors physical features dominating the ecosystem dynamics, (i) the Antarctic Circumpolar Current and (ii) the seasonal sea ice cover region. In the Antarctic, marine predators are exposed to climate-induced shifts in atmospheric circulation and sea ice. However, because these shifts vary regionally, and because much remains to be understood about how individual animals use their environment, it has been difficult to make predictions on how animals may respond to climate variability. Spatio-temporal variability in ecosystem structure and function are likely to translate into modification of top predator population dynamics, however, there is currently a long-standing gap in our understanding of ecosystem functioning under winter Antarctic sea ice. Southern elephant seals (*Mirounga leonina*) are a major consumer of Southern Ocean resources and use two main large scale foraging strategies, (i) feeding in the frontal zone of the Southern Ocean, or (ii) feeding in the seasonal sea ice region. In the present thesis I examined the winter post-moulting foraging strategies of 46 male and female Kerguelen southern elephant seals which utilized the second strategy. Using an eleven year time-series of tracking, diving, and seal-collected hydrographic data (from 2004-2014) we assessed their movements and foraging performance in relation to in situ hydrographic and sea ice conditions. The influence of both the spatio-temporal and inter-annual variability of sea ice around seal locations was investigated, and an investigation on the role of polynya for male southern elephant seal during winter conducted.

Two general sex specific patterns of sea ice usage were observed: females tended to move with the ice edge as it extended northward, and the males remained on the continental shelf despite increasing sea ice. Female foraging activity was greater over shallower seabed depths and at the boundary between the overlying Antarctic Surface Water (AASW) and the underlying Modified Circumpolar Deep Water (MCDW). They also foraged more in the outer part of the pack ice, 150 - 370 km south of the ice edge in late autumn. Within persistent regions of compact sea ice, females foraged most intensively (i) in the highest sea ice concentration at their position, but (ii) their foraging activity was longer when there were more patches of low concentration sea ice around their position (either in time or in space; 30 days and 50 km). The high spatio-temporal variability of sea ice around female positions probably allowed them to exploit concentrated sea ice patches while still having regular access to open water. Despite the lack of information on prey availability, females may exploit the ice algal autumn bloom that sustains meso-pelagic prey in the under-ice ecosystem. They may also take advantage of fishes overwintering at the upper boundary of the MCDW. In marked contrast, the males' foraging effort increased when they were deep within sea ice over the shelf (420 - 960 km from the ice edge). Male foraged most intensively (i) in the lowest sea ice concentration at their position, and (ii) their foraging activity was longer when there were more patches of low concentration sea ice around their position (either in time or in space; 30 days and 50 km). Two distinct foraging strategies were observed for males: (i) Pelagic dives within the Antarctic Slope Front on the continental shelf break where upwelling of nutrient rich Circumpolar Deep Water onto surface water may enhance and concentrate resources; (ii) shallower pelagic and benthic dives within coastal polynyas sustaining biologically rich ecosystems throughout the ice season. For the first time, we demonstrated that coastal polynyas in East Antarctica are "winter oases" for male southern elephant seals spending up to 75 % of their total foraging trip in them. The autumn transition is a key moment in the winter foraging ecology of seals with the highest foraging activity, dive duration and deepest dives observed inside polynyas. The seals may take advantage of the secondary production resulting from the deepening of the seasonal mixed-layer, entraining the remnant deep chlorophyll maximum into the surface layer and presumably stimulating an autumn bloom. Finally, I demonstrate the role of inter-annual variability of near-surface meridional winds, incorporating large-scale climatic variability, in influencing foraging activity of female southern elephant seals through their effects on the timing of sea ice advance. Years of stronger meridional winds may lead to earlier sea ice advance, and both associated with increased foraging activity presumably through trophic cascading effect from enhanced ice algal autumn bloom to southern elephant seal prey.

This work contributes to better understand the ecological mechanisms taking place in the under sampled under-ice ecosystem, while elucidating a crucial part of the annual cycle of a major top predator of the Southern Ocean. It also proposes mechanisms by which climate forcing affects both abiotic and biotic components of the Antarctic marine ecosystem. In the context of the Kerguelen southern elephant seal population, the capacity of seals to employ two foraging strategies (frontal or Antarctic zone strategies) may confer on the population the ability to adapt to short-term (decadal) variations on resource availability, presumably explaining the current stable demographic trend of the population.

Keywords: Elephant seals . Foraging behaviour . Antarctic sea ice . Oceanography . Polynya . Marine ecology . Telemetry

Sous la banquise Antarctique : écologie alimentaire des éléphants de mer des îles Kerguelen, influence des paramètres océanographiques et de glace de mer

Résumé: Les mammifères marins de l'Océan Austral, situés au somment des chaînes alimentaires, sont des éléments essentiels de la structure et du fonctionnement des écosystèmes marins antarctiques et des sentinelles irremplaçables de l'état des océans polaires. Comprendre comment les paramètres océanographiques déterminent leurs habitats préférentiels est essentiel pour identifier de quelle façon et dans quelle région ces mammifères acquièrent les ressources nécessaires à leur déplacement, leur croissance, leur reproduction et donc leur survie. Dans la zone Antarctique recouverte saisonnièrement par la glace, les prédateurs marins sont confrontés à des modifications de la circulation atmosphérique et de la banquise sous l'effet du changement et/ou variabilité climatique. Cependant il demeure difficile de prédire la réponse de ces prédateurs aux variations de leur environnement physique car ces changements sont différents suivant les secteurs de l'Océan Austral et la compréhension de l'utilisation de leur environnement et leur stratégie d'alimentation est encore incomplète. De plus, nos connaissances encore très parcellaires sur le fonctionnement des écosystèmes sous la banquise en hiver limitent notre interprétation de l'influence des variations spatio-temporelles des écosystèmes Antarctiques sur la dynamique de ces prédateurs. Les éléphants de mer du Sud (*Mirounga leonina*) se déplacent dans l'océan austral à l'échelle des bassins océaniques depuis leur colonie subantarctique pour s'alimenter en plongeant en moyenne à 500 m et jusqu'à 2000 m de profondeur. En fonction de leur colonie d'origine, de leur sexe, et de leur âge, ils exploitent des régions radicalement différentes de l'océan austral, mettant ainsi en œuvre des stratégies alimentaires diversifiées. Les éléphants de mer de Kerguelen utilisent deux zones préférentiellement: la zone du Front Polaire ou la zone Antarctique couverte par la banquise. Dans cette thèse, les stratégies alimentaires des voyages post-mue Antarctiques de 46 mâles et femelles éléphants de mer de Kerguelen ont été étudiées. Une série temporelle de 11 années (2004-2014) de données de déplacement, de plongées et de données hydrologiques a été analysée pour déterminer le rôle des paramètres océanographiques et de glaces de mer impliqués dans l'acquisition des ressources alimentaires des éléphants de mer en Antarctique. L'influence de la variabilité spatio-temporelle et interannuelle de la glace de mer associée à la position des mâles et des femelles ainsi que le rôle des polynies côtières sur les stratégies alimentaires des mâles en hiver ont été examinés.

Deux comportements différents entre les mâles et les femelles ont été observés en relation avec la présence de la glace de mer : les femelles suivent la lisière de glace qui s'étend au Nord au cours de la saison mais restent dans la zone dite du "pack" ; en revanche, les mâles restent sur le plateau Antarctique malgré l'extension de la banquise vers le Nord. L'activité alimentaire des femelles, déterminée par un index de temps passé en chasse, est plus longue en Automne proche du plateau Antarctique, dans la partie extérieure du "pack", 150 – 370 km au Sud de la lisière des glaces, et sur la verticale, à la frontière entre l'eau Antarctique de surface et l'eau circumpolaire modifiée (mCDW). Dans un environnement composé de glaces concentrées et persistantes, le temps des femelles passé en chasse est plus important dans les parcelles de glace les plus concentrées, mais associées à de fortes variabilités spatio-temporelles de la concentration de glace (30 jours et 50 km autour de la position). La forte variabilité spatio-temporelle de la glace autour de la position des femelles leur permet probablement d'exploiter des parcelles de glace très concentrées, tout en garantissant un accès régulier à la surface autour d'elles. Malgré le manque d'information sur la disponibilité des proies, j'émets l'hypothèse que les femelles bénéficient indirectement du bloom automnal dans la banquise permettant de soutenir une production secondaire et d'attirer des proies mésopélagiques à des profondeurs moindres sous la banquise. Elles pourraient aussi bénéficier de poissons mésopélagiques se réfugiant en hiver à la frontière entre l'eau froide Antarctique de surface et l'eau circumpolaire modifiée plus chaude et riche en nutriments. Contrairement aux femelles, le temps de chasse des mâles est plus important sur le plateau, lorsqu'ils se trouvent très profondément dans la zone des glaces, entre 420 et 960 km de la lisière. Cependant, le temps de chasse des mâles est plus long dans les parcelles les moins concentrées en glace (à leur position et 30 jours et 50 km autour de la position). Pour les mâles, deux stratégies distinctes d'alimentation ont été observées : (i) des plongées pélagiques dans le courant de pente Antarctique où la remontée d'eau circumpolaire modifiée riche en nutriments en surface pourrait augmenter et concentrer les ressources ; (ii) des plongées peu profondes benthiques et pélagiques dans les polynies côtières soutenant un riche écosystème tout au long de la saison des glaces. J'ai également démontré le rôle important des polynies côtières comme oasis hivernaux pour les mâles éléphants de mer, qui demeurent jusqu'à 75% du temps total de leur voyage alimentaire dans ces zones. La transition automnale semble être un moment clé de l'écologie alimentaire des mâles dans les polynies avec la plus grande activité alimentaire, durée de plongée et profondeur comparés aux autres mois. J'émets l'hypothèse que les mâles exploitent la production secondaire et les proies associées résultant de l'approfondissement de la couche de mélange entrainant la convection du maximum de chlorophylle dans les couches de surface, stimulant ainsi un bloom automnal en juin. Finalement, j'ai démontré le rôle important de la variabilité interannuelle des vents de surface méridionaux, incorporant la variabilité climatique à large échelle, sur l'activité alimentaire des femelles à travers son effet sur la date d'avancée de la glace de mer. Le temps de chasse est plus important les années où les vents soufflant du sud sont plus forts et où la glace se forme plus tôt dans la saison. J'émets

l'hypothèse qu'une formation et une avancée anticipée de la glace, probablement sous l'action des forts vents méridionaux, entrainent l'incorporation d'une plus grande quantité de phytoplancton présent dans la colonne d'eau. Ceci favorise un bloom automnal des algues de glace plus intense et permet par l'intermédiaire de cascades trophiques de soutenir un écosystème plus riche sous la glace et donc d'augmenter l'activité alimentaire des femelles.

Ces travaux de thèse contribuent à une meilleure compréhension des processus écologiques intervenant au sein des écosystèmes vivant sous la banquise tout en élucidant une partie cruciale du cycle de vie d'un prédateur de l'Océan Austral. Ils proposent aussi des mécanismes par lesquels les forçages climatiques affectent les éléments biotiques et abiotiques des écosystèmes marins antarctiques. A l'échelle de la population d'éléphants de mer des Iles Kerguelen, la capacité à maintenir deux stratégies d'alimentation différentes (stratégie frontale ou antarctique) pourrait permettre de compenser les variations décennales de disponibilité des ressources, expliquant probablement la tendance démographique actuelle stable de cette population.

Mots clés: Éléphants de mer du Sud . Écologie alimentaire . Glace de mer Antarctique . Océanographie . Polynie . Écologie marine . Télémétrie

Authority of Access Statement

Statement of Co-Authorship

The following people and institutions contributed to the publication of the work undertaken as part of this thesis:

Candidate, Sara Labrousse, UPMC, LOCEAN (France) and UTAS, IMAS (Australia); **Author 1,** Frédéric Bailleul, SARDI (Australia); **Author 2,** Mark Hindell, IMAS (Australia); **Author 3,** Jean-Benoit Charrassin, LOCEAN (France); **Author 4,** Jean-Baptiste Sallée, LOCEAN (France); **Author 5,** Christophe Guinet, CEBC (France); **Author 6,** Robert Harcourt, MQ (Australia); **Author 7,** Clive McMahon, SIMS (Australia); **Author 8,** Rob A. Massom, ACE CRC, AAD (Australia); **Author 9,** Phillip Reid, BOM, CAWCR (Australia); **Author 10,** Alexander D. Fraser, ACE CRC (Australia); **Author 11,** Will Hobbs, ACE CRC (Australia); **Author 12,** Mike Sumner, AAD (Australia); **Author 13,** Karine Heerah, IFREMER (France); **Author 14,** Jade Vacquié-Garcia, NPI (Norway); **Author 15,** Baptiste Picard, CEBC (France); **Author 16,** Fabien Roquet, MISU (Sweden); **Author 17,** Matthieu Authier, CEBC (France).

Paper 1, "Winter use of sea ice and ocean water mass habitat by southern elephant seals: the length and breadth of the mystery": Located in chapter II: Candidate was the primary author and directed the analysis of the data set used here and shared responsibility for writing the manuscript. Post-processing of the data retrieved from tags was carried out by authors 15 and 16. Authors 3, 4, 13, 14, 17 participated in the data analysis. Authors 2, 3, 4, 5 helped in the interpretation of the results. Authors 1, 2, 3, 4, 5, 16, and 17 shared responsibilities for contributing to the final version of the manuscript.

P**aper 2, "Under the sea ice: exploring the relationship between sea ice and the foraging behaviour of southern elephant seals in East Antarctica": Located in chapter III:** Candidate was the primary author and directed the analysis of the data set used here and shared responsibility for writing the manuscript. Authors 3, 4, 8, 9, 10, 12 participated in the data analysis. Authors 2, 3, 4, 8, 9, 10 helped in the interpretation of the results. Authors 1, 2, 3, 4, 5, 6, 7, 8, 9 and 10 shared responsibilities for contributing to the final version of the manuscript.

Paper 3, "Variability in sea ice cover and climate elicit sex specific responses in an Antarctic predator": Located in chapter IV: Candidate directed the analysis of the data set used here and shared responsibility for writing the manuscript. Authors 4, 8, 9, 10 and 11 participated in the data analysis. Authors 2, 3, 4, 8, 9, 10 and 11 helped in the interpretation of the results. Authors 1, 2, 3, 4, 5, 6, 7, 8, 9, 10 and 11 shared responsibility for contributing to the final version of the manuscript.

We the undersigned agree with the above stated "proportion of work undertaken" for each of the above published (or submitted) peer-reviewed manuscripts contributing to this thesis:

Signed:

Mark Hindell
Supervisor
Institute of Marine and Antarctic Studies
University of Tasmania
Date: _24 October 2016_

Signed:
(Prof Craig Johnson)
Centre Director, Institute of Marine and Antarctic Studies
University of Tasmania
Date: __25 October 2016_

Declaration of Originality

I, Sara Labrousse, declare that this thesis titled, "Beneath the sea ice: exploring elephant seal foraging strategy in Earth's extreme Antarctic polar environment" and the work presented in it are my own. I confirm that:

- This work was done wholly or mainly while in candidature for a research degree at this University.
- Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated.
- Where I have consulted the published work of others, this is always clearly attributed.
- Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work. I have acknowledged all main sources of help.
- Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself.

Statement of Ethical Conduct

The research associated with this thesis abides by the international, Australian and French codes on animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University and by the French Polar Institute (Institut Paul Emile Victor, IPEV) ethical and Polar Environment Committees.

Publications, conferences and fieldwork

Publications

- **May 2015** - Labrousse, S., Vacquié-Garcia, J., Heerah, K., Guinet, C., Sallée, J-B., Authier, M., Picard, B., Roquet, F., Bailleul, F., Hindell, M., Charrassin, J-B., 2015. *Winter use of sea ice and ocean water mass habitat by southern elephant seals: the length and breadth of the mystery.* **Progress in Oceanography** 137, 52–68. doi:10.1016/j.pocean.2015.05.023 Chapter II

- **Submitted March 2016** (under review for **Progress in Oceanography**) – Labrousse, S., Sallée, J-B., Fraser, A.D., Massom, R., Reid, P., Sumner, M., Guinet, C., Harcourt, R., McMahon, C., R., Bailleul, F., Hindell, M., Charrassin J-B., 2016. *Under the sea ice: exploring the relationship between sea ice and the foraging behaviour of southern elephant seals in East Antarctica.* Chapter III

- **Submitted August 2016** (under review for **Scientific Reports**) – Labrousse, S., Sallée, J-B., Fraser, A.D., Massom, R., Reid, P., Hobbs, W., Guinet, C., Harcourt, R., McMahon, C., Bailleul, F., Hindell, M., Charrassin J-B. *Variability in sea ice cover and climate elicit sex specific responses in an Antarctic predator.* Chapter IV

- **In Prep.** – Labrousse, S., Takeshi, T., Fraser, A.D., Bestley, S., Sallée J-B., Sumner, M., Williams, G., Roquet, F., Guinet, C., Harcourt, R., McMahon, C., Bailleul, F., Hindell, M., Charrassin J-B. *Coastal polynyas: a top predator winter oasis in East Antarctica.* Chapter V

- **Submitted October 2016** (for **PLOS ONE**) - Malpress, V., Bestley, S., Corney, S., Welsford, D., Labrousse, S., Sumner, M., Hindell, M. *Bio-physical characterisation of East Antarctic polynyas as key southern elephant seal (Mirounga leonina) foraging habitat.* Appendix E

Conferences

- **September 2013** - Talk at the French national conference on southern elephant seal research, CEBC, France.
- **December 2013** - Talk at the 20^{th} Biennial Conference of the Society for Marine Mammalogy, Dunedin, NZ.
- **September 2014** - Poster at the 5^{th} International Bio-logging Science Symposium, Strasbourg, France.
- **October 2015** - Talk at the French national workshop on the Southern Ocean: Oceanographic circulation interacts with cryosphere and affects biogeochemical cycles and ecosystems (LOAF meeting), Paris, France.
- **December 2015** - Poster at the 21^{th} Biennial Conference of the Society for Marine Mammalogy, San-Francisco, US.
- **February 2016** - Talk at the 2016 Ocean Sciences Meeting, New Orleans, US.
- **April 2016** - Talk at the French national conference on southern elephant seal research, CEBC, France.

Fieldwork

- **August - December 2014** - Field team leader on elephant seals work in Kerguelen Islands during the breeding season (PI: C. Guinet). Retrieval of 11 CTD-Satellite Relay Data Loggers from 8 adult females and 3 juvenile males after their post-moult foraging trips. Deployment of different combinations of tags on 16 post-breeding females. Monitoring of 120 young elephant seals from birth to weaning. During this period, I was responsible of all intravenous and intramuscular anesthesia, blood samples and measurements on adults and pups.
- **Upcoming: January - March 2017** - Field team leader for Weddell seal tagging during the oceanographic cruise of the WAPITI project (Water-mass transformation and Pathways In The Weddell Sea: uncovering the dynamics of a global climate chokepoint from In-situ measurements) funded by the European Research Council (ERC) led by Jean-Baptiste Sallée (CNRS researcher at LOCEAN in Paris) in the Weddell Sea aboard the British Antarctic Survey vessel, the James Clark Ross.

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CHAPTER

I General Introduction

1 The science of ecology

The science of ecology is different from other sciences as most people observed nature and attempted to explain it; most people are ecologists to some extent. But ecology is a complex science organized into three levels: the organism, populations of organisms, and communities of populations; and it often ignores details of the biology of individuals, or the influences of evolutionary life history patterns [Begon et al., 2006]. However, as [Dobzhansky, 1973] said, "Nothing in biology makes sense, except in the light of evolution", and then, as [Begon et al., 2006] said "very little in evolution, and hence in biology as a whole, makes sense except in the light of ecology". On Earth, millions of different species, each with genetically distinct individuals, exist and interact in a highly dynamic world. The challenge for ecology is to develop an understanding of complex questions, by seeking simple patterns and predictions without compromising its complexity [Begon et al., 2006].

Ecological questions depend on the level of organisation being considered. At the level of the organism, ecology studies how individuals interact with their environment. The environment of an organism consists of all external processes influencing the organism, which include abiotic (physical and/or chemical) or biotic (other organisms) components. At the level of the population, ecology is concerned with the presence or absence of species, their abundance or rarity, and with their demographic trends. Community ecology focuses on the composition and organization of ecological communities. The science of ecology also focuses on the flux of energy and matter among biotic and abiotic components leading to a fourth level of organization: the ecosystem which encompasses the communities together with their physical environment [Begon et al., 2006].

Within the framework of this thesis, I study ecology at the level of the organism as a step toward understanding at the population level. Hypotheses will be developed taking into account pathways of energy and matter within the given ecosystem.

2 Marine megafauna foraging ecology

Marine megafauna refers to the large animals living in the sea, including mammals, reptiles, large finfish, and seabirds. Similar to their terrestrial counterparts, marine megafauna have move through their environment to obtain resources, breeding grounds, and mates, to find resting areas or to avoid predation. Movement patterns therefore profoundly impact individual fitness [Bowler and Benton, 2005, Hays et al., 2016]. Studying the foraging ecology of large animals (i.e. a subset of the broader movement studies) is crucial to understand how and where animals acquire resources necessary for locomotion, growth and reproduction. Strong evolutionary constraint leads to the optimization of energy acquisition strategies [Stephens and Krebs, 1986]. Indeed, the optimal foraging theory predicts that the most efficient organisms in competition for resources are more likely to survive; and this selection pressure eventually leads to evolution of organisms highly adapted for acquiring resources in a particular environment or set of circumstances [Perry and Pianka, 1997].

There are several fundamental, but unresolved questions in marine foraging ecology. For example, whether general foraging strategies might explain complex movements at-sea. We still lack a full understanding of the roles of learning, the sensory cues used, environmental drivers in shaping prey distribution and thus the choice of habitat, and how climate change might effect their foraging movements and habitat [Hays et al., 2016]. The effects of learning and memory are often inferred from foraging site fidelity, but quantifying those effects remains challenging [Costa et al., 2011, Fagan et al., 2013]. However, cognitive processes, such as sensory perception (e.g. the ability to sense geomagnetic fields) and memory, are fundamental to make the links between behaviour and environment from many taxa, from a range of habitats, including birds, seals, and turtles [Fagan et al., 2013, Hays et al., 2016]. To cope with the patchiness and heterogeneity of marine resources, large animals presumably rely on specific environmental features in which prey availability might be predictable [Weimerskirch, 2007]. Foraging site fidelity should therefore be strongest when prey distribution or availability is predictable [Weimerskirch, 2007]. Prey distribution and primary production depends on the physical and biogeochemical processes of the ocean, in turn governed by physical oceanographic properties. At different spatial and temporal scales, oceanographic features and processes such as thermal layers, eddies and upwelling zones, currents, frontal systems, seamounts, and the edge of the continental shelf are known to effect the distribution of marine predators. By physically aggregating resources, these processes create areas where prey are abundant and foraging efficiency is increased [Chapman et al., 2004, Bost et al., 2009, Raymond et al., 2015]. Thus, understanding how biotic and abiotic properties of the environment underpin habitat selection of large marine animals is crucial in identifying how and where they acquire resources. Foraging success of large animals controls their individual fitness and drives variation in their vertical and horizontal movements that have both costs and benefits. Within these predictable large-scale regions, individual variation in the timing, plasticity and preferred foraging habitat is still enigmatic, as are the roles of learning versus innate behaviours [Hays et al., 2016]. The risk of predation can also have profound impacts in the choice of foraging habitat [Heithaus et al., 2012] and failure to make this distinction by ecologists could lead to erroneous conclusions, for example confusing refuge areas for dense prey patches.

For all of these reasons, marine megafauna represents ideal models with high heuristic value to study foraging strategies in an heterogeneous environment.

2.1 Impact of climate on marine foraging ecology

Different elements of climate, including extreme atmospheric events, El Niño phenomena, increasing ocean temperatures, modification of sea ice extent and seasonality in polar regions may effect the foraging ecology of large marine animals by changing the abun-

dance, distribution and composition of prey and habitat characteristics such as water temperature, resting, and breeding substrate (see Figure I.1) [Fraser and Hofmann, 2003, Constable et al., 2014, Fleming et al., 2016].

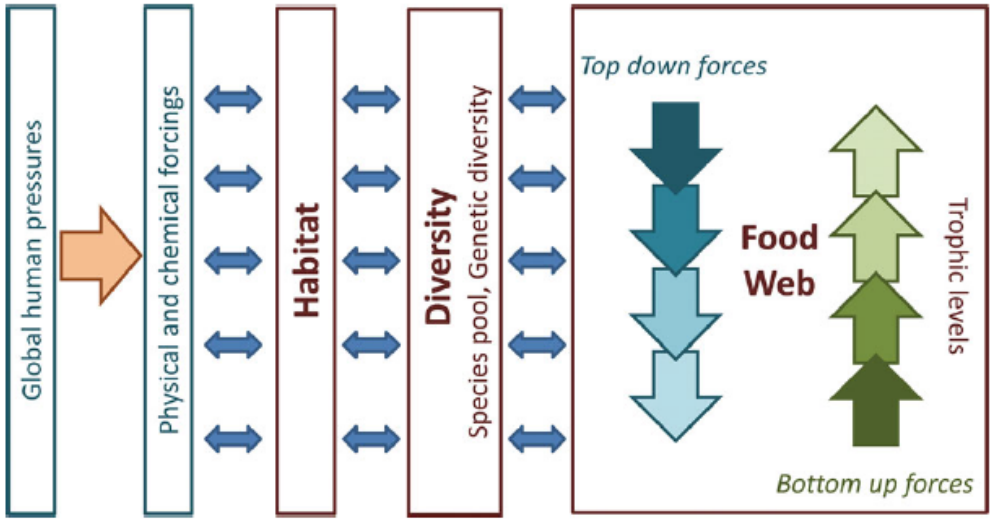


Figure I.1: Schematic from [Constable et al., 2014] illustrating how environmental changes affect habitats, species diversity, and subsequent food webs. The food web is represented by different trophic levels and the number of small horizontal arrows indicates that changes in habitats, diversity, and food webs may occur at any trophic level, leading to both bottom-up and top-down effects.

Movements of marine megafauna are expected to be displaced poleward with warming [Sequeira et al., 2014, Bost et al., 2015]. However, inter-specific competition for resources, plasticity and adaptation of organisms due to changes in habitat availability, for example, can lead to counter-intuitive redistribution in some species [Lyver et al., 2014, Cimino et al., 2016]. Animals dependent upon land-based or ice-based breeding colonies, such as pinnipeds and penguins, might be particularly affected by large-scale environmental changes as they may have a limited ability to shift their foraging locations [Bost et al., 2015]. Another example, is that the rapid loss of sea ice in the Arctic may affect species using sea ice as a platform by restricting their movements, such as polar bears or walruses, or enhancing access to the Arctic for species that were previously stopped by the presence of sea ice [Descamps et al., 2016].

The complexities of an animal's responses to its environment make predictions of climate change effects difficult [Barbraud et al., 2012]. An assessment of potential climate change effects on marine megafauna requires the identification of the oceanographic features and the processes on which these predators rely, coupled with knowledge of how these oceanographic processes are likely to change [Smetacek and Nicol, 2005].

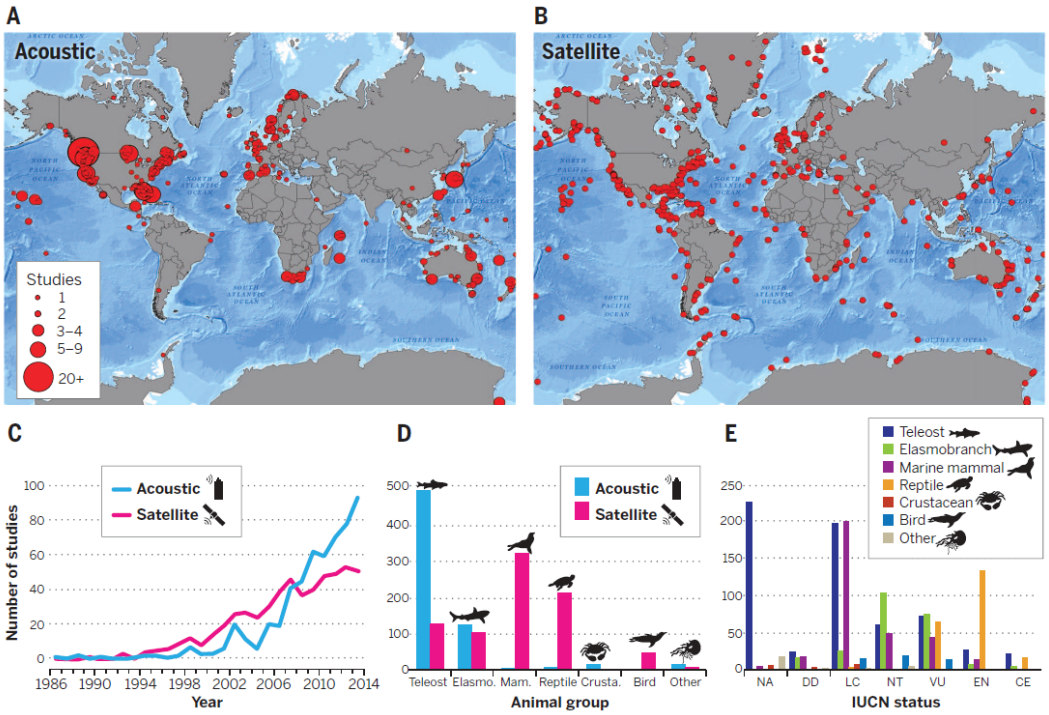


Figure I.2: World distribution of marine telemetry studies from [Hussey et al., 2015]. (A) Acoustic telemetry studies only. (B) Satellite telemetry studies only. (C) Increase in number of acoustic and satellite telemetry studies per year since 1986. (D) Number of acoustic and satellite telemetry studies by major aquatic animal groups (from left to right elasmobranch, marine mammals, crustacean; flightless marine birds only).(E) Number of acoustic and satellite telemetry studies for each major animal group defined by the International Union for Conservation of Nature (IUCN) threat categorization. NA, not assessed; DD, data deficient; LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CE, critically endangered.

2.2 Animal telemetry: tracking and the study of marine megafauna

Historically, the only measure of at-sea abundance, distribution and/or migration of marine animals was provided by the predictable occurrence of commercial species (whaling, sealing and fisheries; e.g. coastally migrating whales, [Clapham et al., 2004]). Technological advances led to the development of biologging (i.e. miniaturised animal-borne tags that can record or transmit data about an animal's movement, behaviour, physiology, and/or environment) in recent decades [Hussey et al., 2015]. These electronic devices can remotely track animals in a diverse range of marine habitats; from the poles to the tropics and ocean surface to the abyssal depths. Biologging allows us to study the horizontal and vertical movements of individuals, populations, and potentially entire communities over different spatial and temporal resolutions ranging from meters to tens of thousands of kilometers and from hours to years (records can even span an animal's entire life at sea). Because radio waves do not propagate in water, marine animal telemetry uses two approaches: acoustic and satellite telemetry (see Figure I.2, [Hussey et al., 2015]).

Electronic tags are equipped with sensors that measure *in situ* physical parameters (e.g. depth, temperature, conductivity, fluorescence, oxygen), as well as the horizontal (track coordinates) and vertical (depth) behaviour of the animal in real time. These data provide invaluable information that give us useful insight into an animal's behaviour and how it interacts with its surrounding environment (see Figure I.3, [Hussey et al., 2015]).

A major task for ecology is quantifying the costs and benefits of various behaviours [Hays et al., 2016], it includes:

- the energy required to pursue a prey, the probability of success and the gain associated with catching it, at the scale of a single event;
- the energy expenditure and benefit of large-scale migration.

Animal-borne sensors show great promise for estimating energy expenditure and intake of animals [Halsey et al., 2009]. For example, energy intake is recorded by stomach or oesophageal temperature sensors measuring the physiological state of the digestion [Charrassin et al., 2001], accelerometers measuring the mechanical movement of the head and/or jaws [Gallon et al., 2013, Naito et al., 2013, Guinet et al., 2014], animal-borne cameras allowing direct observations of prey capture [Watanabe and Takahashi, 2013], and audio recorders to record the sound or echoes of prey capture [Fais et al., 2016]. Metabolic rate and/or energy expenditure can be measured via accelerometers by recording heart rate and body acceleration (e.g. giving information on oxygen consumption [Halsey et al., 2009]) and the flipper stroke effort [Maresh et al., 2015].

Despite the increased development of biologging instruments, linking the benefits of observed foraging strategies to other ecologically relevant parameters (e.g., reproductive success, survival, or population demography) remains an important challenge. Most studies have focused on temporally-isolated events, such as the structure of a single dive or foraging trip. In some cases, tracked animals return to their colony to breed, moult, feed offspring or nest (e.g., seals, seabirds, turtles) so that the benefit from their previous foraging trips can be assessed in terms of their weight change, reproductive investment (e.g. mass at birth of the offspring), and survival across multiple years. It is also sometimes possible to assess changes in body condition, as is the case in some elephant seal studies that record buoyancy changes that can in turn be used to estimate an individual's body condition while foraging at sea ([Biuw et al., 2007, Schick et al., 2013, Richard et al., 2014]). Finally, devices on instrumented animals can also now communicate with one another, providing information into predator-prey interactions and social behaviour.

For these reasons, animal telemetry has considerably increased our ability to study animal movements, interactions, and how the physiological and environmental processes underlying them may affect their foraging strategies, distribution and population dynamic [Hussey et al., 2015].

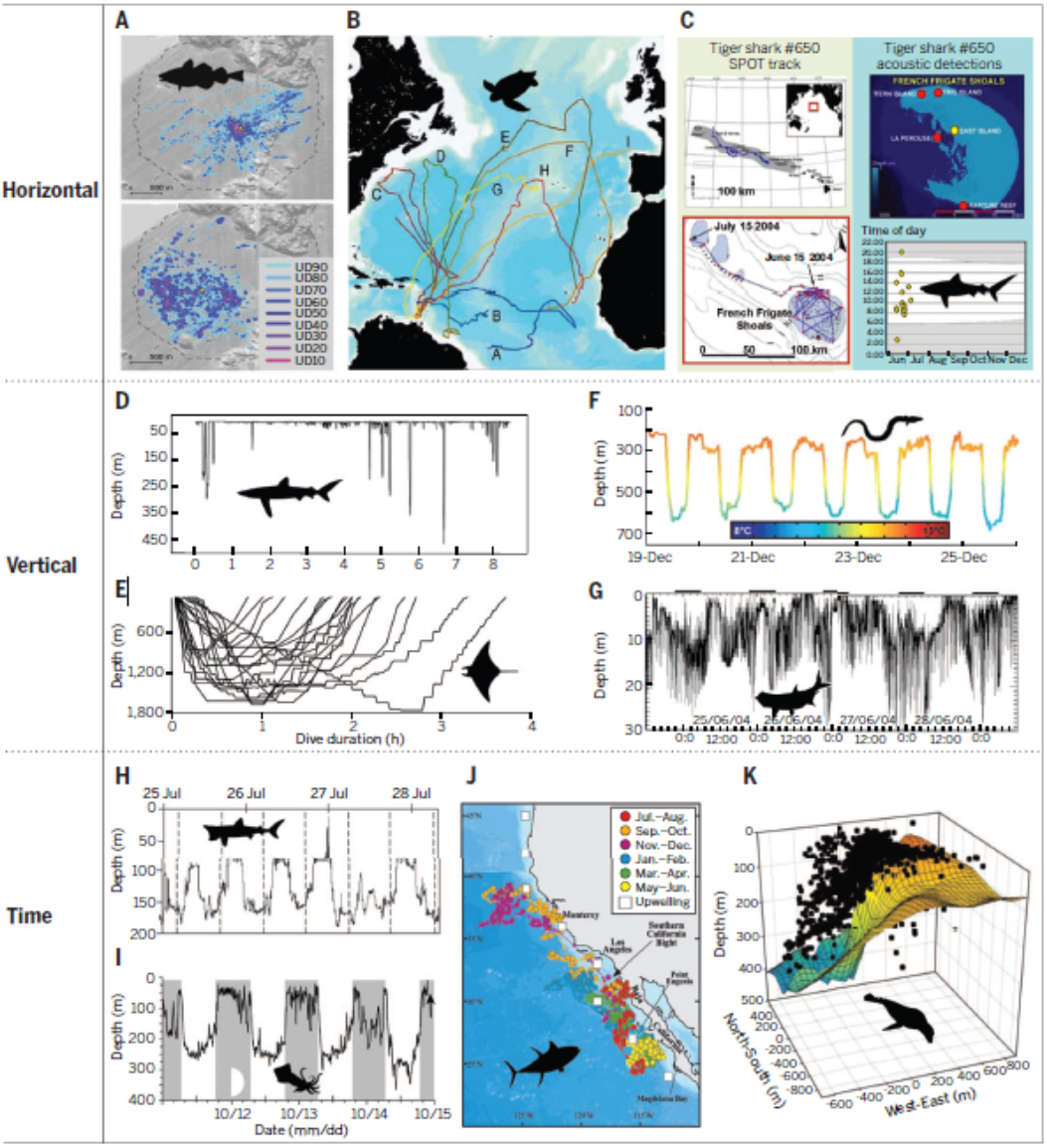


Figure I.3: Marine telemetry reveals animal movements in four dimensions: horizontal (coordinates), vertical (depth), and over time from [Hussey et al., 2015].(A) Fine-scale utilization distribution probabilities of Atlantic cod (*G. morhua*) at their spawning grounds, modified from [Dean et al., 2014]. (B) Transatlantic migrations of individual (A to I) leatherback turtles (*D. coriacea*), from [Hays et al., 2006]. (C) Movements of tiger sharks (*G. cuvier*) from satellite and acoustic telemetry, modified from [Meyer et al., 2010]. (D) Vertical movement behavior of a blue shark (*P. glauca*), modified from [Humphries et al., 2010]. (E) Dive profiles of Chilean devil rays (*M. tarapacana*), from [Thorrold et al., 2014]; h, hours. (F) Oceanic diel migration of a European eel (*A. anguilla*), combined with temperature profile, modified from [Aarestrup et al., 2009]. (G) Dive profile of an Atlantic tarpon (*M. atlanticus*), from [Luo and Ault, 2012]. (H) Tidal-driven vertical movement patterns of a basking shark (*C. maximus*), modified from [Shepard et al., 2006]. (I) Diel vertical movement patterns of a jumbo squid (*D. gigas*), from [Gilly et al., 2006]; mm/dd, month/day. (J) Seasonal spatial utilization patterns by bluefin tuna (*T. orientalis*), from [Kitagawa et al., 2007]. (K) Three-dimensional dive profile of female Weddell seals (*L. weddellii*), from [Hindell et al., 2002] in relation to bathymetry and over two breeding seasons.

3 The Southern Ocean: a unique habitat

The Southern Ocean, defined here as waters south of the Subtropical Front (see Figure I.4), plays a key role in climate and biogeochemical cycles on Earth. It connects the ocean basins and links the overturning thermohaline circulation of the surface and the abysses, that represents a global network of currents, which determines the amount of heat and carbon stored by the ocean [Rintoul, 2011]. The upwelling of deep waters brings nutrient rich water masses into the surface sustaining biological productivity; consequently surface waters sink trapping carbon and heat and also renews oxygen levels (see Figure I.5). The capacity of the world's oceans to buffer against the effects of climate change is strongly driven by the circulation of the Southern Ocean [Rintoul, 2011].

The uniqueness of the Southern ocean comes from the presence of two major physical features dominating the ecosystem dynamics of the region [Constable et al., 2003, Grant et al., 2006, Massom and Stammerjohn, 2010, Constable et al., 2014]:

- (1) The zonal Antarctic Circumpolar Current (ACC) flowing eastward and its frontal systems. The ACC is decomposed in : the Subtropical Front (STF) marking the northernmost extent of the ACC, separating warmer, more saline subtropical waters from fresher, cooler subantarctic surface waters; further south, the majority of ACC water is transported in the Subantarctic Front (SAF), and also in the Polar Front (PF), which marks the transition to very cold and relatively fresh Antarctic Surface Water (AASW), and separates Southern Ocean waters from the Atlantic, Pacific and Indian oceans to the north ([Orsi, 1995]; see Figure I.4 for details). The Polar Front also marks the northerly limit of many non-migrating Antarctic species [Knox, 2006], including Antarctic krill (*Euphausia superba*), the staple food of many of the Southern Ocean seabirds, marine mammals and finfishes. The Southern Boundary of the ACC corresponds to the southern limit of the influence of the ACC.

- (2) The sea ice covered region including the Antarctic shelf and slope regions associated with a complex meridional circulation of water masses (see Figure I.5), the westward flowing Antarctic Slope Current, all influenced by the seasonality of the annual advance and retreat of sea ice (see Figure I.4 with minimum and maximum sea ice extent).

These two large-scale systems make the Southern Ocean a unique natural laboratory to study how environmental processes shape species distribution in the vertical and horizontal dimension and effect marine megafauna behaviour and distribution.

This thesis will study the case of a sub-antarctic deep-diving predator of the Southern Ocean, the southern elephant seal (*Mirounga leonina*). This predator is a unique model species because, depending on age and/or sex, they adopt two different foraging strate-

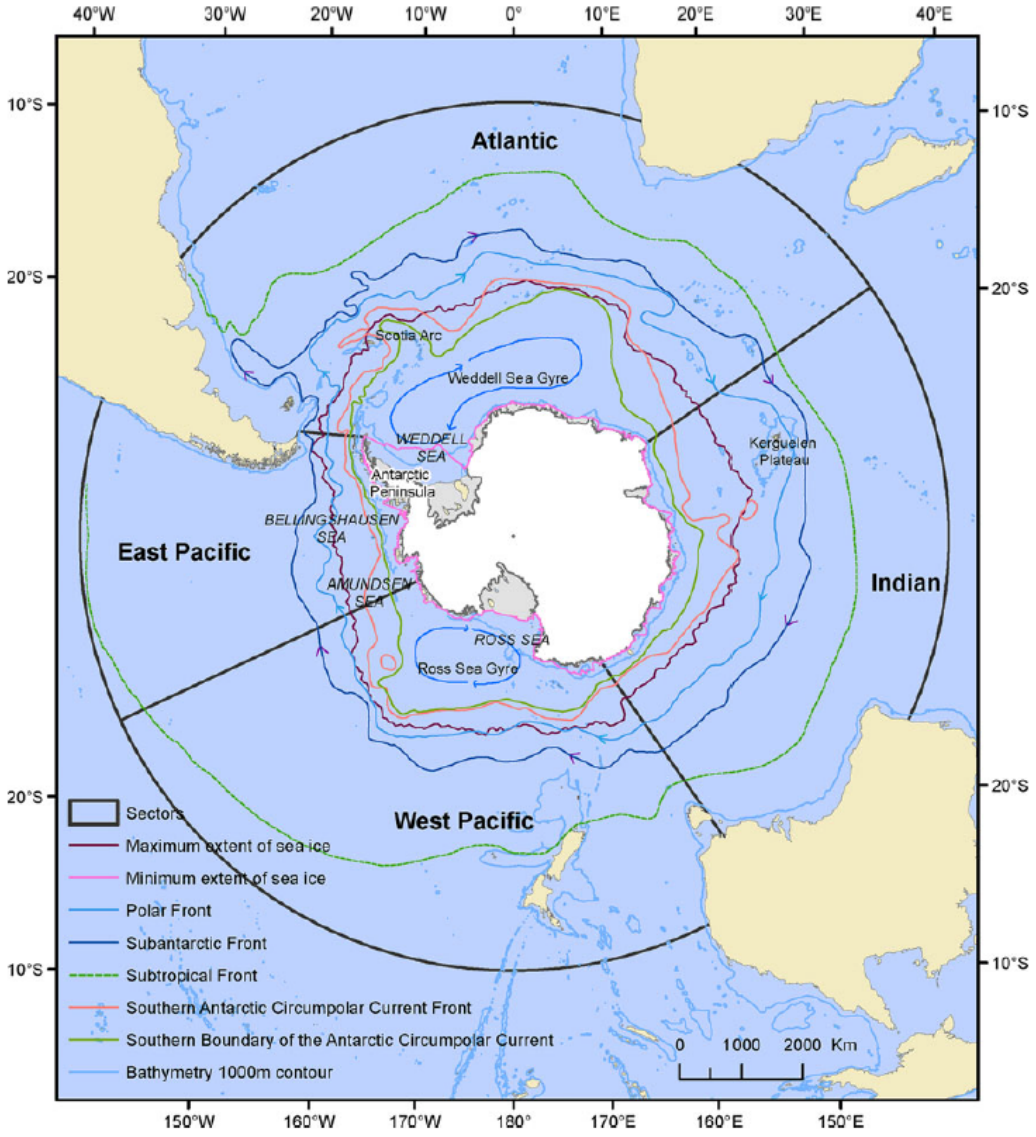


Figure I.4: Illustration from [Constable et al., 2014] representing the major physical features of the Southern Ocean, including major sectors (correspond approximately to an ocean basin, Atlantic, Indian, West Pacific, East Pacific) differentiating the ecosystems, minimum and maximum extent of sea ice, the Subtropical, Subantarctic and Polar Fronts, Southern Boundary of the Antarctic Circumpolar Current, and the 1000 m countour.

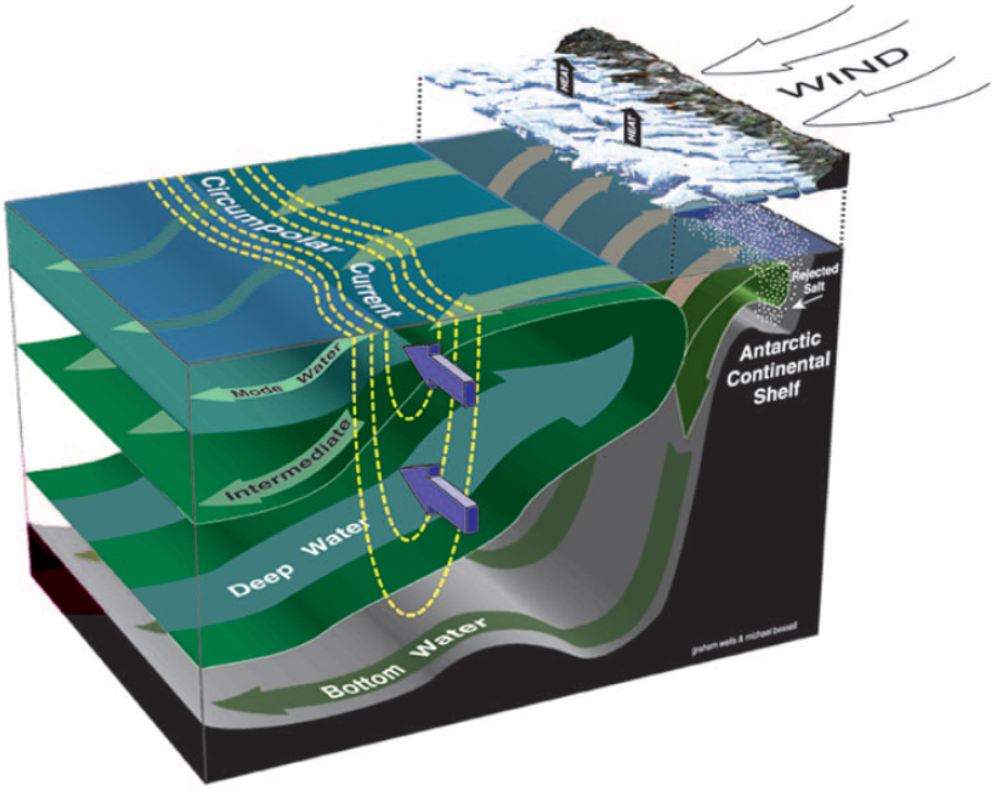


Figure I.5: Schematic representating the Southern Ocean overturning circulation from [Rintoul, 2000]. The figure shows the two cells contributing to the overturning: deep water upwelling to the surface of the Southern Ocean either moves toward Antarctica and sinks to form dense Antarctic Bottom Water, or either moves north and ultimately sinks to depths of 500-1500 m on the northern flank of the Antarctic Circumpolar Current.

gies dependant of the two physical systems described above. They either use the frontal regions of the ACC or either the Antarctic sea ice region as foraging habitat. My research will focus on the latter foraging strategy.

4 South for the winter? Hunting in the dark below the Antarctic sea ice

Antarctic sea ice is a highly dynamic system and extends over a large area of the circumpolar Southern Ocean, ranging from ~ 19 million km^2 in September to ~ 3-4 million km^2 in February [Comiso and Nishio, 2008]. The annual advance/growth and retreat/melting of sea ice is one of the most important physical processes on Earth [Brierley and Thomas, 2002]. By forming a high albedo on the ocean surface, sea ice and its snow cover seasonally modify and affect exchanges of heat and gases between the ocean and the atmosphere, and also the radiative and thermodynamic properties of the ocean surface [Massom and Stammerjohn, 2010]. Salt rejection and freshwater in-

put from seasonal sea ice formation and melt are important determinants of the upper ocean stratification [Martinson, 1990]. In certain key Antarctic coastal areas, the formation of a cold and dense oxygen-rich water-mass (Antarctic Bottom Water, AABW), plays a crucial role in driving the global thermohaline ocean circulation [Orsi et al., 1999, Marshall and Speer, 2012] and represents an important sink for heat, and presumably carbon [Sigman and Boyle, 2000]. Thus, Antarctic sea ice plays a major and variable role in the Earth's climate system.

Sea ice is also plays a key role in the structure and dynamics of Antarctic marine ecosystems and significantly influences all trophic levels that are adapted to its presence, seasonal dynamics and properties [Eicken, 1992, Brierley and Thomas, 2002, Moline et al., 2008, Thomas and Dieckmann, 2009, Massom and Stammerjohn, 2010].

4.1 The ecological importance of Antarctic sea ice

Antarctic sea ice harbors one of the most important ecosystems on Earth, being home of a diverse community of microalgae, bacteria, protists, and the occasional metazoan grazer [Arrigo, 2014]. Enhanced biological activity is associated with both the inside and underside of sea ice and surrounding waters, and is therefore modified by its presence [Brierley and Thomas, 2002]. During its formation, sea ice incorporates dissolved nutrients such as nitrate, phosphate, silicate and trace metal such as iron, which is particularly important for the development of primary producers. Exopolysaccharides produced and utilized by the sea ice microbial community, can be used by sea ice diatoms to grow in both the light and dark; a crucial advantage under conditions of light limitation or during overwinter survival (reviewed by [Arrigo, 2014]). Thus, sea ice significantly contributes to primary production by serving as a substrate for the development of algal biomass in winter; and upon its melt in spring-summer by affecting nutrient dynamics, ocean stratification and light availability resulting in extensive phytoplankton blooms [Arrigo et al., 2008b, Smith and Comiso, 2008, Massom and Stammerjohn, 2010].

The under ice habitat containing sea ice algae provides a key food source for the grazing of herbivorous zooplankton such as juvenile krill and other crustaceans [Marschall, 1988, Flores et al., 2011, Flores et al., 2012b, David et al., 2016] during winter time when food resources are scarce in the water column (see Figure I.6).

Increased secondary production within the sea ice zone attracts and is exploited by upper trophic levels such as deep-water finfish migrating to shallow depths or seals, seabirds and whales [Eicken, 1992, Van Franeker et al., 1997, Reid and Croxall, 2001, Brierley and Thomas, 2002, Tynan et al., 2010, Fraser and Hofmann, 2003]. It affects reproductive cycles, recruitment and foraging behaviour for a wide range of species (reviewed by [Massom and Stammerjohn, 2010]). Finally, sea ice also serves as a key habitat, refuge and barrier to marine predators [Tynan et al., 2010].

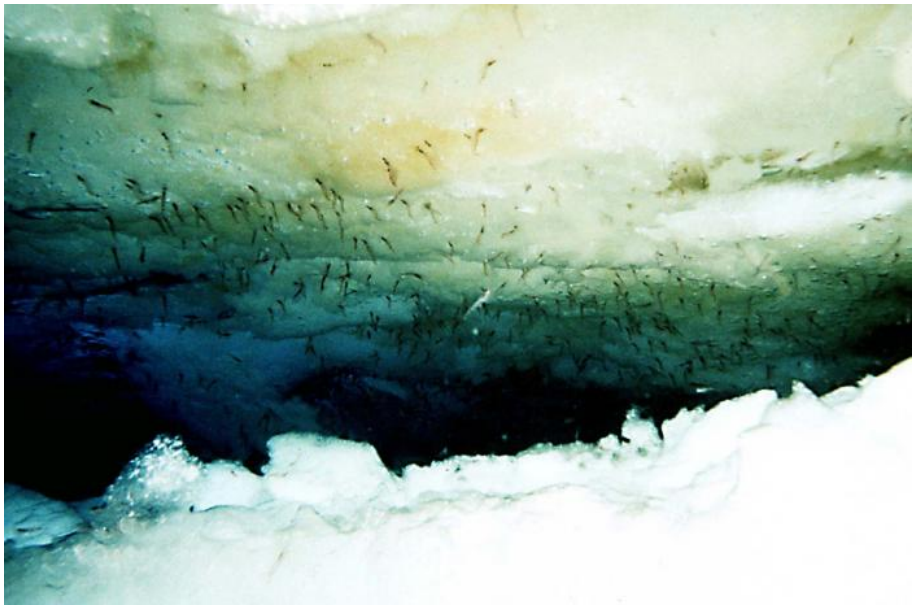


Figure I.6: Photograph, taken by a remote operated underwater vehicle (or ROV), illustrating how most krill feed by swimming upside-down directly under the ice, grazing as they move (photograph courtesy Alfred Wegener Institute).

4.2 Zonation of the Antarctic sea ice environment

The sea ice cover is made up of three zones with distinct characteristics (see Figure I.7 ;[Massom and Stammerjohn, 2010]). These are (from north to south):

- The highly-dynamic marginal ice zone (MIZ), which typically extends 100-200 km or so south from the ice edge, and is generally made up of small floes and diffuse ice conditions (depending on wind direction);
- The inner pack ice zone (PIZ) comprising larger floes separated by leads;
- A coastal zone comprising the band of compact landfast (fast) ice and persistent and recurrent areas of low-concentration sea ice in the form of polynyas and flaw leads.

The MIZ is characterized by high sea ice variability in time and space, as well as enhanced biological activity due to sea ice melt and breakdown releasing an important quantity of food resources (i.e. ice algae) under the strong influence of storms, wind action and ocean wave-ice interaction processes [Wadhams, 2000, Massom et al., 2006, Karnovsky et al., 2007, Squire, 2007, Massom and Stammerjohn, 2010].

The inner PIZ is constituted by an important ephemeral network of leads, made by divergent sea ice conditions in response to storms and currents. Leads are relatively narrow, but they can extend for hundreds of kilometres and constitute "highways" [Massom and Stammerjohn, 2010] which, along with polynyas, allow breathing-

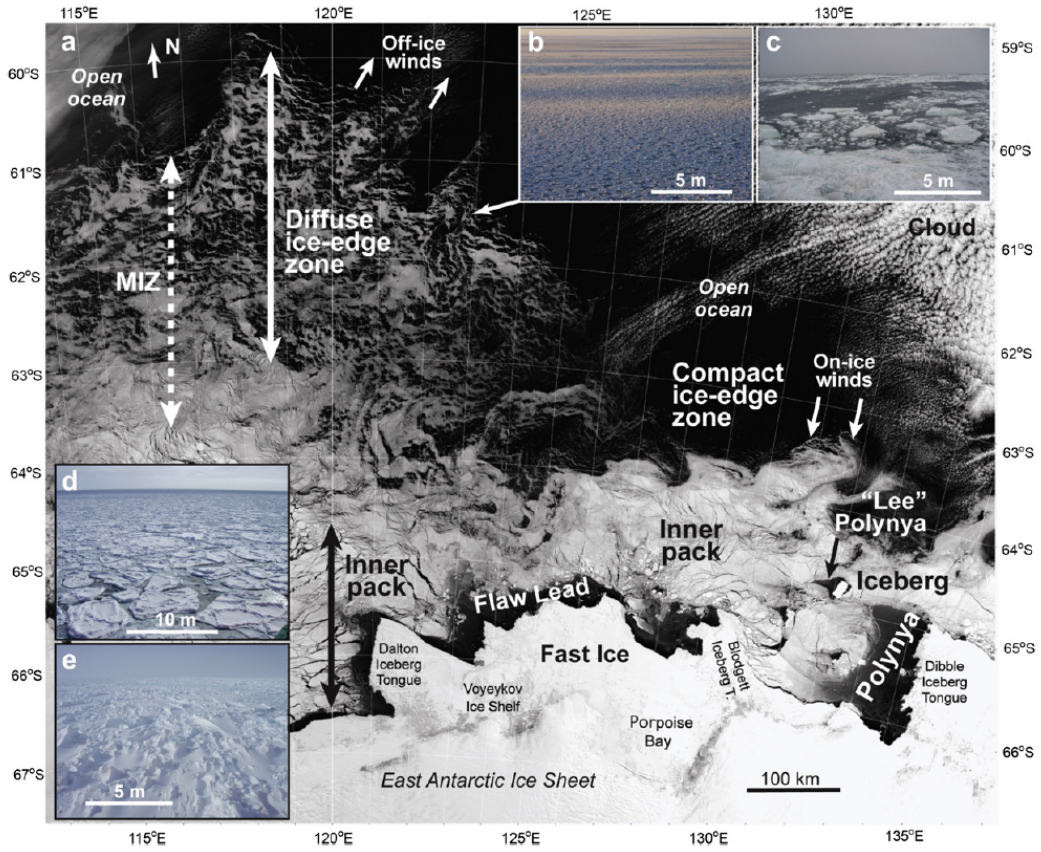


Figure I.7: Illustration from [Massom and Stammerjohn, 2010] representing the different types of sea ice. a) NASA Terra MODIS satellite visible image (resolution 250 m) of the East Antarctic sea ice zone from ~ 112 to 137°E (image courtesy NASA). Panels b, c, d, e are photographs taken from a ship and illustrating the different sea ice conditions present in winter: b) pancake ice formation in the marginal ice zone (MIZ) with ocean wave; c) brash ice and floe fragments close to the ice edge zone; d) thin first-year ice deeper in the pack with a thin snow cover, with small floes fragmented by wave-ice interaction; and e) heavily-deformed thick first year ice with a thick snow cover in the inner pack ice zone.

access for mammals and an ocean-access for birds within the sea ice zone in winter [Bluhm et al., 2010]. These open water areas can sustain high biological activity in spring-summer.

Polynyas are persistent regions of open water and/or thin ice or low sea ice concentration, ranging from tens to tens of thousands of square kilometers in surface extent [Barber and Massom, 2007]. According to their mechanism of formation and maintenance, polynyas have been traditionally divided into two classes: "sensible heat" and "latent heat" polynyas (see Figure I.8).

Sensible heat polynyas are thermally formed and are the result of oceanic sensible heat melting sea ice or preventing its formation in the area of polynya formation. Sensible heat polynyas are therefore locations of low sea ice production, and their size is determined by the amount of warm water creating them [Morales Maqueda, 2004]. In contrast, latent heat

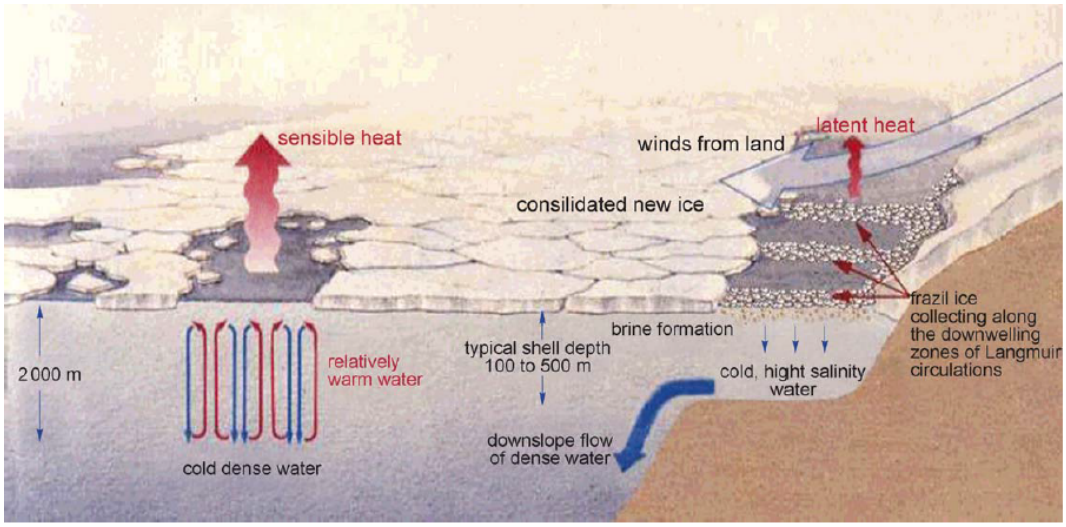


Figure I.8: Schematic from [Colling and Open University. Oceanography Course Team., 2001] redrawn by [Morales Maqueda, 2004] representing physical processes taking place in sensible heat and latent heat polynyas. Sensible heat polynyas occur on the continental shelf break and are formed by upwelling or vertical mixing of subsurface water which leads to sea ice melting or preventing its formation. Latent heat polynyas are over the Antarctic shelf. The majority of these polynyas are wind-driven. Offshore winds push the pack ice away from the coast, exposing the freezing surface waters to the cold atmosphere. Frazil ice is thus formed and advected away by wind. Salt-rich, cold water associated with sea ice formation accumulate over the shelf and likely flow down the shelf break slope to form deep and bottom water.

polynyas are mechanically formed in regions of divergent sea ice due to dominant winds, oceanic currents, and/or barriers (e.g. ice shelves, icebergs) blocking the passage of pack ice, and promoting the formation of new sea ice from the heat lost from the ocean to the atmosphere [Morales Maqueda, 2004, Tamura et al., 2016]. Because the water inside the polynya is normally at the freezing point and heat is lost across the air-ocean interface, ice is continually formed in the polynya region and advected away [Morales Maqueda, 2004]. **In this thesis, I will only refer to latent heat polynyas.**

4.3 Marine predators of the Antarctic sea ice region

Antarctic marine predators, birds and mammals, are defined in three different groups based on their reliance on sea ice [Tynan et al., 2010] :

- Sea ice obligate species, are always found near sea ice; they depend on ice as a floating substrate for resting, breeding, weaning pups and refuge from marine predators. They are: crabeater seals (*Lobodon carcinophagus*), leopard seals (*Hydrurga leptonyx*; they can also occur along subantarctic island coastlines as juveniles), Weddell seals (*Leptonychotes weddellii*), Ross seals (*Ommatophoca rossii*), emperor penguins (*Aptenodytes forsteri*), Adélie penguins (*Pygoscelis adeliae*) and snow petrels (*Pagodroma nivea*);

- Sea ice intermediate species, those who are not obligate but have developed/evolved specific morphological, physiological or behavioural adaptations to exploit sea ice habitat. These are minke whale (*Balaenoptera bonaerensis*), killer whale (*Orcinus orca*), southern elephant seal (*Mirounga leonina*), Antarctic petrel (*Thalassoica antarctica*) and south polar skua (*Catharacta maccormicki*);

- Sea ice non-obligate species, are found often in the open PIZ but ice is largely a barrier to them, such as Antarctic fur seal (*Arctocephalus gazella*), blue whale (*Balaenoptera musculus*), fin whale (*Balaenoptera physalus*), humpback whale (*Megatera novaeangeliae*), sperm whale (*Physeter macrocephalus*), king penguin (*Aptenodytes patagonicus*), blue petrel (*Halobaena caerulea*), Wilson's storm-petrel (*Oceanites oceanicus*), southern giant fulmar (*Macronectes giganteus*) and Antarctic fulmar (*Fulmarus glacialoides*).

Sea ice obligate pack ice seals (crabeater, leopard, Ross and Weddell) and the emperor penguin use sea ice as a platform for reproduction, giving birth or laying eggs in winter or very early spring, and offspring become independent of parents when food availability is highest during late summer and early fall.

Polar species (both seabirds and seals) complete their moult within a few weeks and sea ice obligate species use ice platforms during this period. Moulting penguins are fasting while most seals continue to feed (mostly at night) but spend longer periods of the day hauled out. Volant seabirds, such as snow and Antarctic petrels (practically flightless during the moult), use strong and persistent winds to fly and spend a lot of time sitting on icebergs or large ice floes.

Emperor penguins and Weddell seals require stable fast ice for breeding, and reliable ice floes for moulting [Tynan et al., 2010]. All other pack ice seals (crabeater, leopard, Ross) tend to avoid areas of consolidated pack ice where freeze-ups are frequent and restrictive [Ribic et al., 1991]. Crabeater and leopard seals are predominantly species of the deep pack ice through most of the year. In contrast, Ross seals, despite being an ice obligate species, they have a fully pelagic behaviour during several months, spending about 70% of their time from 500 to 1000 km from the ice edge. They hauled out in the deep pack ice only mainly during the moult in December–January, and in late October–mid-November during breeding [Arcalís-Planas et al., 2015].

From late summer to the end of the winter, southern elephant seals occur within the Antarctic sea ice zone. Although they mate, breed and moult in sub-antarctic islands, a significant proportion of them spent time foraging within the Antarctic sea ice region in winter. **These foraging trips will be the subject of this thesis.**

Minke and humpback whale residence times in Antarctic waters both show rapid increases in late December, while blue and fin whales show a more gradual migration. Recent studies suggested that some of baleen whales are present in the Antarctic year round although there is still little evidence as surveys are difficult during the winter season. Compared with other marine mammals (e.g. Weddell seals), whales have limited capacity to

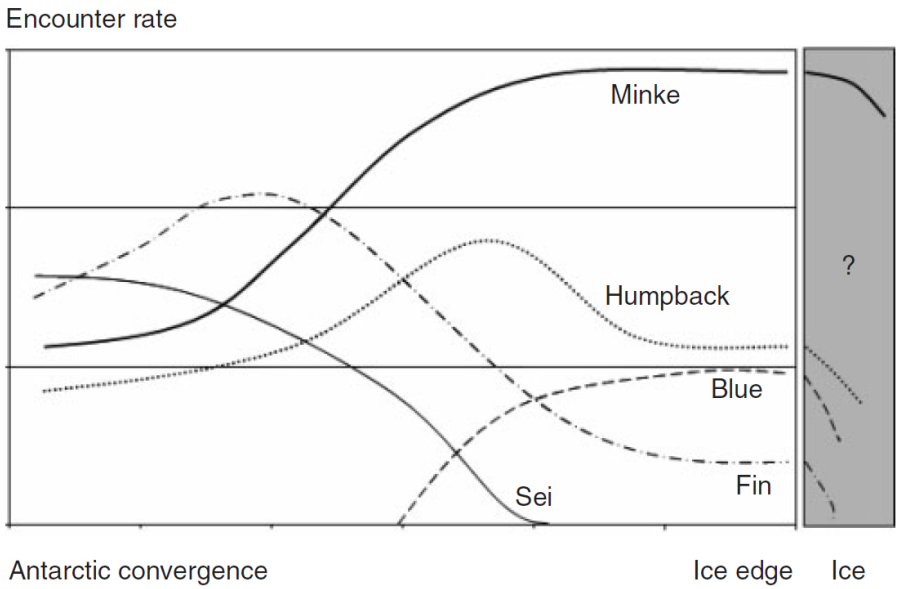


Figure I.9: Latitudinal occurrence of Antarctic baleen whales from [Nicol et al., 2008].

make breathing holes through ice [Nicol et al., 2008]. In the winter pack ice, only the minke whale has been sighted among baleen whales (see Figure I.9). Their small size allows them to enter inside the pack ice zone and access to krill which is not easily accessible to larger baleen whales. In addition, their ability to filter feed large quantities of krill provides an advantage over other smaller krill predators such as penguins and seals that feed on individual prey [Friedlaender et al., 2014].

Like blue and minke whales, humpback and fin whales are also defined as Antarctic krill specialists, but are much less associated with sea ice habitats and continental shelf areas; instead regarded as being more oceanic-dwelling (reviewed by [Nicol et al., 2008]). At least two different ecotypes of killer whales are currently present near or within the Antarctic sea ice region, referred to as types B and C [Pitman, 2011]. Type B killer whales, called "pack ice killer whales" are found around the entire continent where they forage mainly among the pack ice. Type C killer whales, called "Ross Sea killer whales", are known only from East Antarctica where they live deep in the pack ice and use leads (cracks) in the fast ice, often far from open water.

Finally, sei whale (*Balaenoptera borealis*) and southern right whale (*Eubalaean australis*), "type A" and "type D" killer whales respectively, are not, or are rarely, seen close to the sea ice edge and were therefore omitted from the description above.

4.4 The Antarctic ecosystem

The trophic transfer of energy through an ecosystem is usually visualized by the food chain concept. In food chains, energy in the form of organic carbon is mostly assimilated by photosynthesis and then transmitted through a series of consumers feeding on each other. The different steps in the food chain are referred to as trophic levels. At each step of the trophic chain, 80-90 % of the energy and biomass are lost [Knox, 2006]. The food web consists of a complex suite of food chains interacting with each other in an ecosystem with top predators at the highest trophic level of the food web. Marine food webs are usually complex systems with multiple trophic interactions at various levels.

4.4.1 Antarctic pelagic assemblages

The pelagic ecosystem of the seasonal ice zone does not differ greatly from the basic pattern of the typical marine food web following the phytoplankton-zooplankton-nekton-top predator trajectory. However, a unique characteristic of the sea ice pelagic ecosystem is the unusually high abundance of a micronektonic phytoplankton consumer, the Antarctic krill (*Euphausia superba*). The energy flow through the intermediate trophic levels can follow two main pathways in the Southern Ocean (see Figure I.10):

- Antarctic krill is a major trophic link between the primary producers and the upper trophic levels;
- Evidence of a second major trophic pathway from phytoplankton to mesopredators in the pack ice region during autumn was emphazised by [Flores et al., 2011, David et al., 2016], via macrozooplankton and micronekton under winter sea ice (mainly copepods and myctophids), including intermediate trophic steps via cephalopods and large finfishes [Flores et al., 2008]. This suggests that the copepod - finfish - top predator link is probably as important as the more widely documented krill pathway.

Antarctic krill ((*Euphausia superba*); zooplankton) is an extremely effective grazer capable of depleting phytoplankton blooms over short periods of time (e.g. [Ross et al., 1998]). The vertical distribution of Antarctic krill during winter is poorly understood due to the lack of data from the sea ice zone in winter. The first multi-seasonal study of the distribution of Antarctic krill in the upper 2 m layer of the ocean used a micronekton net sampling under pack ice and found that Antarctic krill populations can be found in the ice-ocean upper layer almost year-round, both close to the ice edge and hundreds of kilometres deep in the pack ice [Flores et al., 2012b]. As algal biomass in sea ice is considerably greater than in the underlying water column in winter [Quetin and Ross, 2009], sea ice represents a crucial habitat for postlarval krill (i.e. juveniles), and larvae are assumed to depend on ice algae to survive their first winter [Marschall, 1988, Massom and Stammerjohn, 2010,

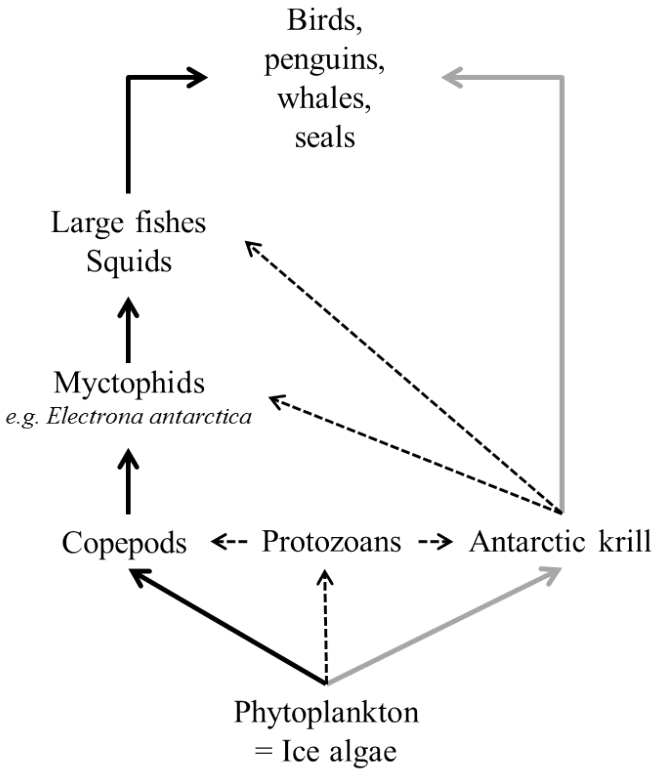


Figure I.10: Illustration adapted from [Flores, 2009] of major pathways of the pelagic food web in the oceanic seasonal sea ice zone of the Southern Ocean. The copepod-finfish/squid trajectory is indicated by black, the krill trajectory by grey arrows. Trajectories included in the two pathways are represented by dashed lines.

Flores et al., 2012b, Schaafsma et al., 2016]. Older krill stages may however show a different response to the sea ice environment. There are significant seasonal differences in the association of Antarctic krill with sea ice (see Figure I.11;[Flores et al., 2012b]):

- In summer, postlarval Antarctic krill in the 0–2 m surface layer are more abundant under the melting sea ice than the open ocean surface layer;

- In autumn, postlarval Antarctic krill in the 0–2 m surface layer are more abundant in the open ocean surface layer than under the ice. In this season, the young sea ice is unlikely to harbour a sufficiently abundant microbial community for postlarval krill. In contrast, larval Antarctic krill were significantly more abundant under the young autumn sea ice than in open ocean surface layer. During periods of low food availability, larval Antarctic krill are not able to actively move into the more productive waters of the open ocean. Thus, even in young autumn ice, they were found to forage on sea ice algae. This suggests different distribution patterns of adult and larval Antarctic krill when food availability is low;

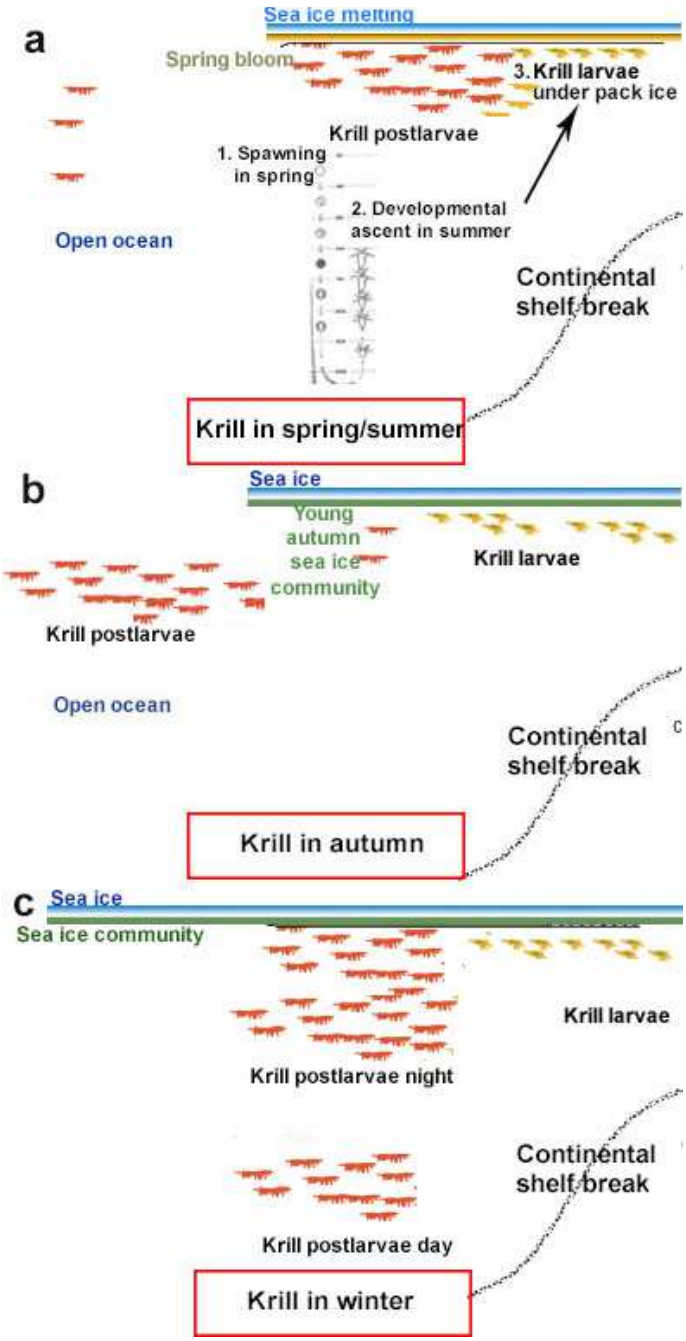


Figure I.11: Simplified seasonal representation of the vertical and horizontal distribution of Antarctic larval and postlarval krill outside (left) and inside sea ice (right) adapted from the results of [Flores et al., 2012b] and inspired by [Nicol, 2006]: (a) spring-summer, (b) autumn, and (c) winter.

- In winter, the highest densities of postlarval Antarctic krill were encountered under the sea ice. Several exceptionally high densities of postlarval Antarctic krill were observed with values exceeding maxima found within the integrated 0–200 m depth layer. This indicated that Antarctic krill were associated with the under-ice habitat at certain periods of the season. The absence of Antarctic krill under the sea ice at day versus high densities at night indicated that the association with the under ice may be limited to the dark hours in winter. Krill might combine various strategies to survive the winter, such as reduced metabolism, shrinkage and benthic feeding. Thus the role of sea ice algae in winter may be crucial to krill only when other food sources are not available. Also, postlarval Antarctic krill may particularly depend on winter feeding, because they have less storage capacity and metabolic plasticity than older animals.

In contrast with past knowledge on the krill cycle, Antarctic krill are also found in the surface layer across all seasons, rather than just confined to deeper layers in autumn and winter (see Figure I.11). In turn, krill is a key component of an under ice ecosystem up to mesopelagic areas by transferring the energy to the pelagic food web through vertical migration, food chains and sinking detritus (reviewed by [Brierley and Thomas, 2002]).

The apparent dominance of Antarctic krill in the pelagic ecosystem led to the initial conclusion that the food web has a simple structure, from krill to higher trophic levels. This view was formed during the 1970s and 1980s, where major ecosystem studies concentrated their efforts in the economically-important Antarctic peninsula/Scotia Arc region (e.g. [El-Sayed, 1994]). In this region, bathymetry and currents enhance the concentration of krill which may have led to the misunderstanding of the overall ecological relevance of krill [Flores, 2009]. Indeed, the broader Antarctic krill population is unable to graze more than 5 % of the total primary production [Knox, 2006], leaving enough resources for the copepod - nekton pathway.

In the Southern Ocean, the mesopelagic ichthyofauna is composed of 73 species belonging to 24 families [Kock, 1992], and are both dominated in terms of species number and biomass, by the family of Myctophidae or lanternfishes [Barrera-Oro, 2002]. Lanternfishes mainly feed upon mesozooplankton [Pakhomov et al., 1996, Pusch et al., 2004] and represent an important part of the diet of various bird and mammal species [Barrera-Oro, 2002, Cherel et al., 2008]. In the region south of the Antarctic Polar Front, the myctophid *Electrona antarctica* is the dominant species of both fish larvae (with *Notolepis coatsi*, Antarctic jonasfish) and postlarvae [Morales-Nin et al., 1995, Hoddell et al., 2000, Fisher et al., 2004, Lancraft et al., 2004, Donnelly et al., 2006], and also the most abundant lanternfish [Sabourenkov, 1990]. Through diel vertical migration, *E. antarctica* efficiently transfers energy between the mesopelagic and epipelagic zones in both directions [Flores et al., 2008]. Also, about 24 to 70 % of the biomass of *E. antarctica* from 0-1000 m depth in high Antarctic pelagic waters, was found to occur in the upper 200 m at

night [Lancraft et al., 1989, Donnelly et al., 2006]. Thus, *E. antarctica* may represent an alternative pathway in the pelagic food web similar in terms of energy magnitude to krill [Flores et al., 2008].

Other abundant mesopelagic and epipelagic finfishes, are the families Bathylagidae (deep-sea smelts) and Paralepididae (barracudinas). The deeper-dwelling bathylagid *Bathylagus antarcticus* for example, is found at depths down to 4000 m, but displays vertical migration up to the surface layer [Lancraft et al., 1989, Parkes, 1992]. Similarly, the paralepidid *Notolepis coatsi* (Antarctic jonasfish) inhabits waters from surface to 2000 m depth [Parkes, 1992].

Most early stages of Antarctic finfish species are usually epipelagic with larvae of Bathylagidae, Myctophidae and Paralepididae commonly found in oceanic near surface waters [Hoddell et al., 2000, Fisher et al., 2004].

Finally, while mesopelagic finfish usually inhabit deeper waters in ice-free open water areas, in the pack ice areas they are found directly below the sea ice [Kaufmann et al., 1995, Brierley and Thomas, 2002]. Examples of mesopelagic finfish found directly below sea ice include myctophid (*Electrona antarctica*, [Lancraft et al., 1991, Quetin and Ross, 2009]), swarms of young and adult bald notothen (*Pagothenia borchgrevinki*), Antarctic toothfish (*Dissostichus mawsoni*) and Antarctic silverfish (*Pleuragramma antarcticum*), [Fuiman et al., 2002, Bluhm et al., 2010].

4.4.2 Antarctic shelf assemblages

Antarctic krill have been intensively studied in the pelagic and slope waters of the Southern Ocean [Siegel, 2005, Nicol, 2006], but surprisingly little is known about mesozooplankton (greater than 200 mm) in the shelf system and their role in the transfer of energy in Antarctic shelf assemblages. The zooplankton grazer crystal krill (also known as ice krill; *Euphausia crystallorophias*) is an obligate ice form and the single most important grazer of neritic diatoms [Pakhomov and Perissinotto, 1996]. However, its quantitative relationship with ice algae is still poorly known[Smith et al., 2007]. Crystal krill are presumed to be an important trophic link between the sea ice biota with the underlying water column community, due to their importance in the diets of upper trophic levels [Smith, Walker O. et al., 2014]. The study of [Sala et al., 2002] reported that crystal krill dominated on the continental shelf while Antarctic krill was dominant near the shelf break. During late spring / early summer, crystal krill is presumed to be depleted by mesopredators (e.g. Adélie penguins, Antarctic silverfish and minke whales, who then switch their diet to small finfishes during summer [Ainley et al., 2006, Ainley et al., 2015a]. During the summer/fall transition, the Antarctic silverfish become cannibalistic, feeding on their own larvae [Eastman, 1985], suggesting that this feeding behaviour may result from crystal krill becoming seasonally depleted. Thus 'wasp-waist' food webs predominate in continental shelf ecosystems as detailed by [Frank et al., 2007].

Figure I.12: Antarctic toothfish are an important food item for Weddell seals, photography from Jessica Meir.

In Antarctic shelf waters, the notothenioid Antarctic silverfish dominates pelagic fish species [White and Piatkowski, 1993, Hoddell et al., 2000, Granata et al., 2002] from surface to ~ 900m [Daneri, G.A. and Carlini, 2002, La Mesa et al., 2010]. Differences in spatial repartition is likely to occur between the different life stages of Antarctic silverfish; larvae feed on zooplankton in the surface layer of the shelf waters and move into deeper layers farther offshore when they become juveniles. Mature adults then return to the shelf for spawning [Maes et al., 2006].

Antarctic silverfish is the prey of multiple different Antarctic species such as volant birds (South polar skuas, snow petrels and Antarctic petrels), Adélie and emperor penguins, Weddell seals, Antarctic toothfish and other finfishes, minke and killer whales [Smith et al., 2007]. Thus, in the relative absence of crystal krill, Antarctic silverfish may become the dominant route of energy transfer through the water column [Smith et al., 2007].

The cryopelagic notothenioid Bald notothen is also common in Antarctic shelf waters, and live in the upper 6 m of the water column, often on the underside of sea ice, that they use as a refuge to avoid predation. Emperor penguins, skuas and Weddell seals are their main predators [Smith et al., 2007].

The epibenthic notothenioid Antarctic toothfish [Bradshaw et al., 2003, Smith et al., 2007] is the largest finfish in Antarctic waters. Juveniles are principally found on the shelf while adults are found along the slope [Ashford et al., 2012] sometimes shallower than though within the sperm whale (*Physeter macrocephalus*) and southern elephant seal dive range of 1000 m [Watwood et al., 2006] or under fast ice in mid-depths [Fuiman et al., 2002]. This piscivore feeds heavily upon Antarctic silverfish [Eastman, 1993] and is, in turn, the prey of whales [Thomas et al., 1980] and seals (see Figure I.12, [Testa et al., 1985]).

Blue and minke whales are generally defined as Antarctic krill specialists [Kawamura, 1994], although both species can also consume other krill species. These two baleen whale species are the most associated with sea ice (pagophylic) and the continental shelf and shelf break areas [Kasamatsu et al., 2000, Murase et al., 2002]. They occur mainly in southernmost latitudes, concentrating nearby the edge of the pack ice [Kasamatsu et al., 1998, Branch et al., 2007] and in the case of minke whales sometimes

within the pack ice itself. In the most southern waters, they can also feed upon the Antarctic silverfish in addition to crystal krill (e.g. the south-east shelf of the Ross Sea), particularly in years of low sea ice extent [Ichii et al., 1998].

Type A, B and C of killer whales can be encountered on the shelf. As detailed in subsubsection 4.3, type A mainly feed on Antarctic minke whales, type B mainly feed on seals or penguins, and type C on Antarctic toothfish [Pitman, 2011].

Seabird populations also have high biomass in the Antarctic shelf, such as Adélie and emperor penguins, and antarctic and snow petrels [Smith et al., 2007].

Pinnipeds are composed of five species, the crabeater seal (*Lobodon carcinophagus*), Weddell seal, leopard seal (*Hydrurga leptonyx*), Ross seal (*Omatophoca rossi*) and elephant seal (*Mirounga leonina*, [Tynan et al., 2010]). All of these apex predators feed principally on the Antarctic silverfish and crystal krill in shelf waters [Eastman, 1985, Eastman, 1993, Ichii and Kato, 1991, Cherel and Kooyman, 1998, Tynan et al., 2010]. Weddell seals also feed heavily on the Antarctic toothfish [Testa et al., 1985, Kim et al., 2005].

Finally, Antarctic benthic communities are characterized by an important biomass, biodiversity and endemism [Clarke, 2008] and a strong resistance to change in species composition [Brey and Clarke, 1993]. For these reasons, they are among the most ecologically stable communities in the world.

A simplified illustration of the major pathways of the Antarctic shelf food web is represented in Figure I.13.

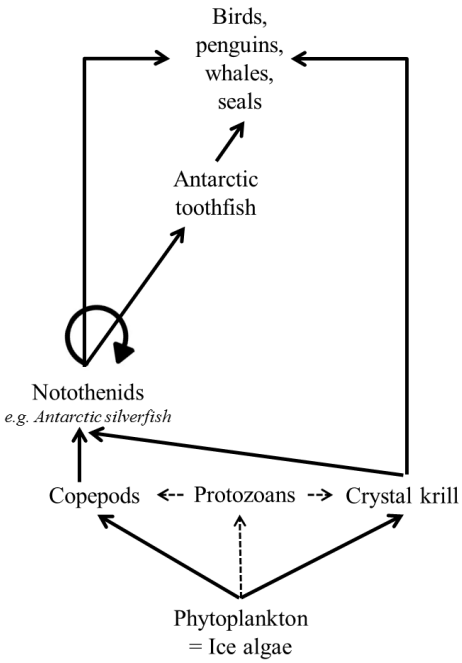


Figure I.13: Illustration adapted from the results of [Smith et al., 2007] of major pathways of the shelf food web in the seasonal sea ice zone of the Southern Ocean.

4.4.3 Antarctic shelf break assemblages

The Antarctic slope front largely matches with the shelf break, forming an effective physical barrier separating offshore pelagic communities of mesopelagic finfishes and shelf-associated communities of notothenioids in the Southern Ocean. Near the shelf break, Antarctic krill, myctophid finfish and the glacial squid (*Pyschroteuthis glacialis*), replace crystal krill in the diets of top predators [Smith et al., 2007].

4.4.4 Life in polynyas

Surface waters of polynyas are the first polar marine systems in spring to be exposed to solar radiation, either because they are not covered by sea ice or either because their weak ice cover may breakout early in spring, often leading to biologically productive waters [Arrigo and van Dijken, 2003]. The resulting phytoplankton blooms persist even after sea ice has disappeared in summer, generally sustaining the highest phytoplankton biomass on the relatively productive continental shelf [Arrigo and van Dijken, 2003]. Rates of primary production often exceed 1 g C m^{-2} [Arrigo et al., 2000]. While these blooms happen between early spring and summer, Antarctic coastal polynyas are a site of concentrated biological activity with rich ecosystems that support large populations of mammals that are able to breathe and feed throughout the ice season [Arrigo and van Dijken, 2003, Karnovsky et al., 2007, Tremblay and Smith Jr., 2007, Tynan et al., 2010, Arrigo et al., 2015]. Polynyas also support rich benthic communities such as sponges, echinodermes, crustaceans and cnidarians [Ambrose and Renaud, 1995] through an enhanced vertical carbon flux ([Grebmeier and Barry, 2007]. The dominant zooplankton grazers in this ecosystem include microzooplankton, copepods, krill and salps [Li et al., 2001, Pakhomov et al., 2002].

While the importance of polynyas as a site of concentrated biological activity is now widely accepted, our understanding of these ecosystems is still based on relatively few studies. One chapter of this thesis will focus on the use of polynyas by southern elephant seals in an attempt to fill this gap.

4.5 Seasonality of Antarctic primary production

The dynamics of Southern Ocean ecosystems are driven by highly seasonal physical characteristics (see Figure I.14): in winter, solar radiation and water temperature decrease while the mixed layer depth, nutrients, and sea-ice cover increase [Constable et al., 2014]. These parameters control the availability of light and nutrients for the primary production. In Antarctica, phytoplankton blooms are observed close to the sea ice edge when sea ice retreats during spring and summer [Arrigo et al., 2008a], and can also occur within the sea ice itself [Massom et al., 2006] (see Figure I.14).

Assessment of primary production at large-scales is derived from satellite estimates of chlorophyll a, based on ocean-colour observations in the open ocean. However, ice-covered regions masked the ocean preventing estimates of primary produc-

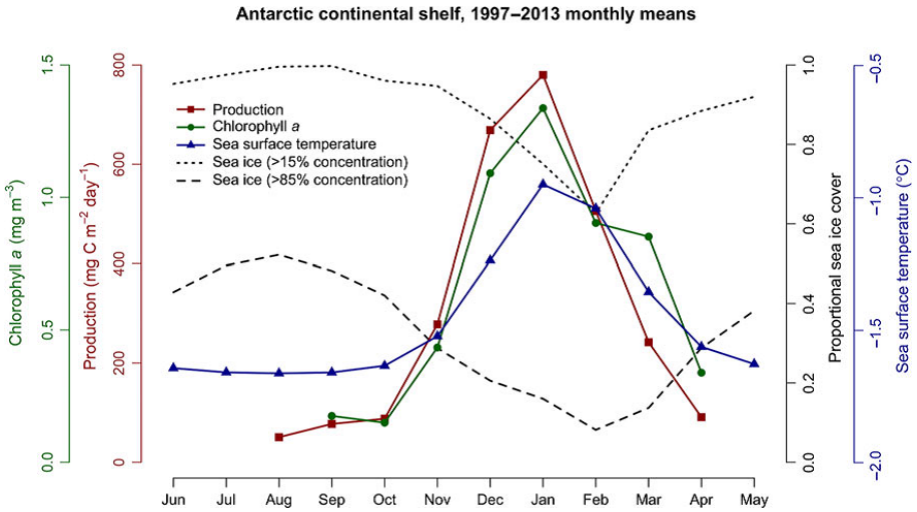
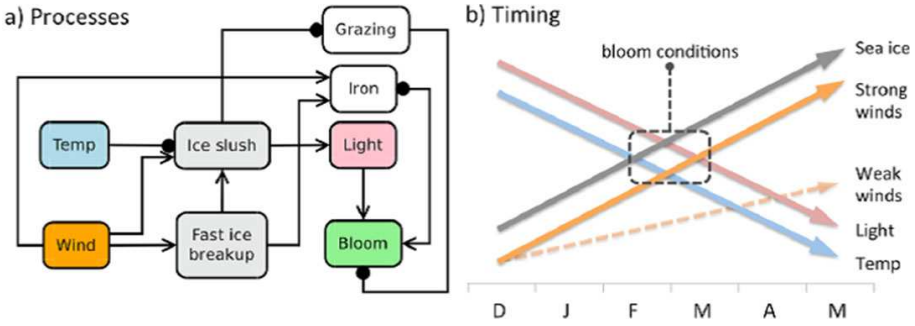


Figure I.14: Mean annual cycles for primary production, chlorophyll a, sea surface temperature and sea ice over the Antarctic continental shelf from [Constable et al., 2014].

tion [Massom et al., 2006, Bélanger et al., 2007]. In autumn, declining solar radiation reduces incoming photosynthetically active radiation, fall mixing reduces stratification leading to entrainment of phytoplankton to depths with limited light, and lower temperatures allow sea ice growth further attenuating light in the ocean. These changes limit the growth of primary production which then declines in the Antarctic sea-ice zone (e.g.[Arrigo et al., 2008b]).

However, autumn blooms in consolidated sea ice have been observed around Antarctica [Fritsen et al., 1994, Lieser et al., 2015], including within ice floes in the pack ice zone [Meiners et al., 2012]. This contradicts the assumption that primary production is negligible in the sea ice region during early autumn [Smith Jr. et al., 2000]. Specific conditions likely to favour early autumn ice-associated blooms in the Southern Ocean are detailed in figure 4.5.

Ice algal autumn blooms are generally not intense, but they are biologically significant and could provide a readily accessible food source for pelagic herbivores such as krill, which may in turn sustain upper trophic levels in autumn/early winter season [Meiners et al., 2012]. In polynyas, primary production in early spring/summer presumably extends feeding and reproduction in zooplankton (such as copepods and euphausiids) into late summer and early autumn [Deibel and Daly, 2007]. Similarly, middle to upper trophic levels might benefit from this secondary production and concentrated resources through the autumn/early winter season. The current neglect of an autumn bloom from non-detection of ice-associated phytoplankton in conventional satellite ocean-colour images may have also underestimate the potential of sea ice to sustain a rich under ice ecosystem during winter [Lieser et al., 2015].



illustrating the interactions between parameters leading to conditions favouring early autumn ice-associated blooms in the Southern Ocean.]Conceptual model from [Lieser et al., 2015] illustrating the interactions between parameters leading to conditions favouring early autumn ice-associated blooms in the Southern Ocean. On panel a, connections terminated by an arrow indicate a positive effect while those with a filled circle indicate a negative effect. Two-ways feedback is also possible. Decreases in atmospheric temperature (blue) and increases in wind (orange) promote the formation of ice slush, which, together with iron released from wind-induced upwelling and fast ice breakup, promotes the formation of early autumn blooms (green). Panel b represents the corresponding timing of changes in levels of light, sea ice, atmospheric and sea-surface temperature and wind strength for the Cape Darnley region between December and May. Optimal conditions for bloom formation overlap in late February/early March.

4.6 Hydrological conditions in the Antarctic shelf

As detailed in the section 3, the ACC allows the exchange of water masses between the different ocean basins and between the surface and deep depths in the Southern Ocean. Towards Antarctica, deep and intermediate Circumpolar Deep Water (CDW) arise close to the surface. Exchanges of heat and freshwater with atmosphere and sea ice leads to the transformation of water-mass densities. It creates lighter water-mass such as Subantarctic Mode Water (SAMW) and Antarctic Intermediate Water (AAIW) respectively, as well as dense Antarctic Bottom Water (AABW). CDW transforms into modified Circumpolar Deepwater (mCDW) south of the Southern Boundary and then moves along the Antarctic shelf break to the shelf region. Dense Shelf Water (DSW) also called High Salinity Shelf Water (HSSW) forms with the cooling of shelf surface layers and brine-rejection from sea ice growth in coastal polynya regions around the Antarctic shelf. In the vicinity of the shelf break, Dense Shelf Water (DSW) mixes with mCDW, it becomes modified Shelf Water (mSW) moving across the shelf break down the continental slope. Under specific physical properties, such as negative buoyancy, this mSW will produce AABW ([Hindell et al., 2016], see Figure I.16). On the shelf, the mSW is called LSSW.

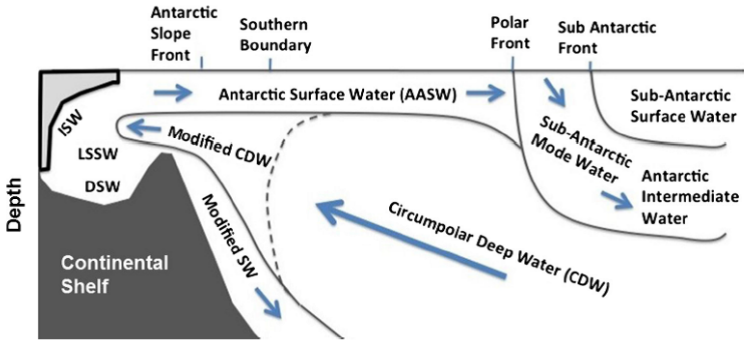


Figure I.16: Schematic illustration from [Hindell et al., 2016] of the vertical organisation of the major water masses in the Antarctic shelf. Abbreviations: SW, Shelf Water; ISW, Ice Shelf Water; DSW, Dense Shelf Water; LSSW, Low Salinity Shelf Water, similar to mSW but south of the shelf break.

4.7 Changes in Southern Ocean and its ecological implications

Over the last three decades, the structure and function of Antarctic and Southern Ocean marine ecosystems have been changing in response to increasing ocean temperatures [Gille, 2008], freshening of water masses [Durack and Wijffels, 2010], strengthening of westerly winds, with a likely pole-ward displacement of those winds [Bracegirdle et al., 2008] and the frontal systems [Moore et al., 1997], increasing ocean eddy activity [Meredith and Hogg, 2006] and changes in the extent and seasonality of sea ice [Parkinson and Cavalieri, 2012, Stammerjohn et al., 2012]. These changes effected the whole food web, phytoplankton, zooplankton such as Antarctic, crystal krill and copepods, finfish, cephalopods, marine mammals, seabirds and benthos. Lower trophic levels are likely to move south as the oceanographic properties of their habitat are displaced pole-ward. Regarding Antarctic krill and finfish, their tolerance to changes in ocean temperatures, primary productivity and sea ice extent and dynamics will determine their latitudinal range [Massom and Stammerjohn, 2010]. Ocean acidification is already affecting calcifying organisms but may also have implications for the physiology of crustaceans such as Antarctic krill. Change in the sea ice conditions may have the most important effects on benthic assemblages through change in seasonal primary production, modifying the quantity, quality, timing and duration of the seasonal input of organic matter from the spring bloom [Lohrer et al., 2013]. For seabirds and marine mammals, the degree by which they will be influenced by changes in the Southern Ocean is dependent upon their flexibility in moving to alternative foraging grounds and the energy expenditure of longer or more complex foraging trips for those that are central place foragers, tied to land-/ice-based breeding colonies (reviewed by [Constable et al., 2014]).

Regional contrasting trends in changes are observed in each sectors of the Southern Ocean :

- The Western Antarctic Peninsula (East Pacific sector in Figure I.4; WAP) is warming at one of the fastest rates on Earth, with simultaneous changes in the populations at the upper levels of the ecosystem. Around the WAP, the air has warmed by 3.4°C per century [Vaughan and Marshall, 2003]; whereas in the Bellingshausen Sea, the sea surface has warmed by 1°C since 1950 [Meredith and King, 2005]. Meanwhile, several major ice-sheets collapsed, numerous glaciers have retreated, and major changes in sea ice have occurred [Clarke et al., 2012]. In the WAP region, the annual mean sea ice extent has decreased by ~ 7% per decade and the ice season duration has shortened by ~ 30 days per decade since 1979 [Stammerjohn et al., 2012]. As for most Antarctic regions, consequences of sea ice reduction and increase in surface temperature on ice-based predators is still poorly known;

- In contrast to the WAP region, the neighbouring Weddell Sea (Atlantic sector in Figure I.4) has in large parts been an area of net increase in sea ice coverage over the past 3 decades. In its north-western parts, however, the sea ice season has been markedly shortening [Stammerjohn et al., 2012]. This region is directly influenced by waters advected from the west by the ACC. It is also an area of high krill abundance [Atkinson et al., 2009], and contains important breeding colonies of Antarctic birds and seals as well as key foraging grounds of baleen whales, and target areas of the fishery. In spite of a recent overall sea ice increase, several signs of ocean warming suggest a reversal in this trend in the coming decades. Climate warming induced the collapse of the Larsen A and B ice shelves along the eastern coast of the Antarctic Peninsula (e.g. [Scambos et al., 2000]). Coupled sea ice-ocean models predict a decline of about 2/3 of the sea ice volume in the Weddell Sea by the end of the 21^{st} century, causing in combination with other factors a re-direction of current patterns and rapid melting of the ice shelves on the southern coast of the Weddell Sea [Hellmer et al., 2012]. These changes have the potential to significantly alter the structure and spatial distribution of ecological provinces in the Weddell Sea. Besides changes in sea ice habitats of the open ocean, new habitats may become available by vanishing ice shelves, opening retreat areas for communities otherwise endangered by climate change [Gutt et al., 2011];

- The Ross Sea (West Pacific sector in Figure I.4) contrasts with the WAP in terms of physical settings, regional sea ice trends, and their relationships with top predators. The WAP continental shelf is continuously ventilated by nutrient-rich Upper Circumpolar Deep Water (UCDW) from the ACC. In contrast, the Ross Sea is isolated from the ACC by the large Ross Gyre and the strong westward-flowing Antarctic slope current [Smith, Walker O. et al., 2014]. The gyre-originated UCDW is upwelled on the large shelf via several troughs. Strong katabatic winds drive the very large Ross Sea Polynya and high primary production in ice-free waters. The Ross Sea proves to be the most productive region of the coastal Southern Ocean, accounting for 25% of its CO2 sink [Arrigo et al., 2008b]. This may remain high all year long because herbivorous zoo-

plankton are maintained at a low level by the very large populations of top predators, thereby reducing diatom grazing [Ainley et al., 2006]. In contrast to the WAP, sea ice extent in the Ross Sea has been increasing at 5% per decade over the past 30 years [Turner et al., 2009], coincident with the positive phase of the SAM.

- East Antarctica features a strong inter-annual variability in sea ice extent and krill abundance. There was a slight increase in sea ice extent in the last 30 years (1.7% per decade), no clear trend in krill biomass, and contrasting top predator biological responses [Turner et al., 2009, Nicol and Raymond, 2012, Massom et al., 2013]. This sector (~30°- 150°E) includes two main regions separated by the Kerguelen Plateau, where the large-scale ocean circulation controls sea ice extent and defines two broad krill habitats, which differ in their northward extension, defined by the Southern Boundary of the ACC (SbACC,[Nicol and Raymond, 2012]). The SbACC front separates the cold westward-flowing coastal Antarctic current from the ACC is mirrored by the winter ice extent. More details for this sector could be found in section 6.4.

For the purpose of this thesis, I will focus on changes in sea ice characteristics and seasonal dynamics and its effects on marine predators (marine mammals and seabirds) foraging within the Antarctic sea ice region.

4.7.1 The case of Antarctic sea ice

Sea ice coverage over the past 37 years in the Southern Ocean shows a small but statistically-significant overall increase [Zwally et al., 2002, Comiso and Nishio, 2008, Parkinson and Cavalieri, 2012, Hobbs et al., 2016]. However, as detailed in section 4.7, there are contrasting trends at the regional scale with increased sea ice coverage in the western Ross Sea (i.e. West Pacific sector, see Figure I.4), strong decreased sea ice coverage in the Bellingshausen and Amundsen seas (i.e. East Pacific sector) and related trends in yearly duration [Liu et al., 2004, Stammerjohn et al., 2012]. Sea ice is effected by many different processes in the atmosphere and ocean. These include the transport of heat, the displacement of sea ice by wind and ocean currents, and freshwater input in the mixed layer such as precipitation, salt rejection and meltwater from icebergs, ice shelves and marine-terminating glaciers. These processes could have different possible role in driving the observed trends described above, here is a summary from the review of [Hobbs et al., 2016]:

- Atmospheric processes, such as wind, are believed to explain most of the observed interannual variability and the trends in sea ice. Depending on their direction, meridional winds transport warm, moist air from lower latitudes or cold, dry air from the continent, affecting sea ice growth and melt. Wind is also the major driver of sea ice movements;

- Snowfall accumulation pushes the ice surface below sea level, the resultant immersion creates a slush layer that can subsequently freeze into sea ice. Thus, snow ice formation is an efficient way of thickening the ice or maintaining its thickness;
- Changes in storm activity and location may modify sea ice conditions, and observations suggest fewer but more intense cyclones in the sea ice zone in the future;
- Under anthropogenic pressure, a shift towards a positive phase of the Southern Annular Mode (SAM; the dominant mode of atmospheric variability over the Southern Ocean, which can be defined as the intensity of the zonal winds; [Thompson and Wallace, 2000]), and a concomitant increase in circumpolar westerlies is observed over the Southern Ocean. This leads to sea ice initially expanding, but over longer time-scales this drives Ekman transport of warm Circumpolar Deep Water into the surface reducing sea ice growth;
- Although zonal winds (mainly the SAM) is the dominant feature of the Southern Ocean atmosphere, the relative effect of meridional winds on sea ice coverage is important. This is due to the thermally driven meridional transport of sea ice, which is much greater than its zonal equivalent;
- One of the most important features of the atmospheric meridional transport influencing sea ice trends is the Amundsen Sea Low (ASL), a quasi-stationary atmospheric low pressure anomaly. Around this low pressure centre, cyclonic air-mass drives warm poleward winds into the Antarctic Peninsula/Bellingshausen Sea region, and a cold equatorward wind over the Ross Sea, with implications for the dipole in sea ice trends between these two regions;
- Antarctic sea ice also strongly responds to tropical sea-surface temperature anomalies via the El-Niño Southern Oscillation (ENSO), due to weakened ASL during warm ENSO events (i.e. El Niño), and the contrary during La Niña. However, the influence of the ENSO teleconnection is only statistically significant when SAM is in a weak (i.e. neutral) phase, or when SAM is in phase with the driving ENSO event (i.e. El Niño with negative SAM, La Niña with positive SAM).
- Sea ice forms when ocean water is cooled below its freezing point, and so the key primary ocean variable controlling sea ice formation is the temperature of the surface mixed layer. As the temperature of the mixed layer is tied to the stratification of the water column, it means that relationships between ocean stratification and sea ice freeze/melt may be important in explaining the overall increase in sea ice and its regional and seasonal characteristics.
- Finally, freshwater input from melting ice shelves could change the water column stratification sufficiently to cause an expansion of sea ice cover, this hypothesis is still under debate.

Understanding sea ice changes, its regional variability around Antarctica, the complex interplay of its atmospheric and oceanic drivers, and their relationship with climate change is still a significant and important scientific challenge [Hobbs et al., 2016].

Changes in sea ice extent and seasonality have implications for ecosystems as sea ice plays a crucially important role in the structure and function of Southern Ocean ecosystems [Thomas and Dieckmann, 2009, Massom and Stammerjohn, 2010]. Antarctic predator populations do not respond in a uniform way around Antarctica, and contrasting trends are observed that reflect regional differences in sea ice change and variability and in species ecology and biological requirements [Massom and Stammerjohn, 2010, Constable et al., 2014, Southwell et al., 2015].

A review of the present and predicted effects of sea ice changes on predators around Antarctica could be found in Table I.1. In this review, whales are represented by only one study as changes in survival and/or reproductive performance in response to sea ice changes is difficult to assess for whales in absence of long-term demographic data compared with other vertebrate predators, such as seals and seabirds [Nicol et al., 2008].

The response of predators is governed by their physiological plasticity to tolerate change, adapt to new environmental conditions or migrate to alternative foraging grounds that enable survival.

As stated by [Ducklow et al., 2007], "a major challenge involves not only documenting ecosystem responses at all levels of biotic organization (genome to planetary), but also establishing a mechanistic understanding of the linkages between climate, sea ice, biogeochemical processes and lower to upper trophic levels". In the present thesis, I identify the linkages between an Antarctic mesopredator and oceanographic and sea ice processes (i.e. chapter II). I then focus on the influence of the variability of sea ice on their movements and foraging ecology (i.e. chapters III and IV).

4.8 Sea ice, a double-edge sword: constraints and benefits

Marine birds and mammals, relate to sea ice in three ways [Tynan et al., 2010]:

(1) Sea ice provides a physical habitat for sea ice obligate species with resting platforms and breeding grounds;

(2) Sea ice provides access to a rich food source during autumn-winter time;

(3) Sea ice can be an impediment for air-breathing marine predators, because of the physical barrier it builds between the ocean and air. For example, higher temporary emigration rates of young and old female Weddell seals was presumably directly due to limitations in their ability to navigate under extensive sea ice to access breeding colonies, committing them to costly long swim beneath sea ice [Chambert et al., 2015]. Moreover, several studies based on emperor penguin already suggested an optimum level of ice cover with neither complete absence of sea ice nor heavy and persistent sea ice providing satisfactory conditions for sea ice dwelling species [Tynan et al., 2010, Barbraud et al., 2012, Jenouvrier et al., 2012].

Table I.1: Review of the present and predicted effects of sea ice changes on predators around Antarctica. EA refered to East Antarctica, SG for South Georgia, WAP for Western Antarctic Peninsula, RS for Ross sea, WRS for Western Ross sea , WWS for Western Weddell sea and C for circumpolar.

Change in sea ice	Effects on marine predators / Area	Species	References
Increase in pack ice extent	Positive on adult survival; Negative on fecundity (1952 to 2000) / EA	Emperor penguins	[Barbraud and Weimerskirch, 2001]
Long-term reduction in sea ice extent leading to reduction in krill population	Decline in all species and increase in the frequency of years of low reproductive output / SG	Antarctic fur seal, gentoo penguin, macaroni penguin, black eye-browed albatrosses	[Reid and Croxall, 2001]
Sea ice-driven change in krill recruitement and availability	Direct link between sea ice, krill and predator foraging / WAP	Adélie penguins	[Fraser and Hofmann, 2003]
Shift in conditions during mid-early 1970s and again during 1988-89	Prediction of increase of Adélie penguin population if continued warming and stronger winds (larger Ross sea polynya); decrease in emperor penguins due to thinner fast ice during winter, more rapidly decaying ice in spring / WRS	Adélie, emperor penguins	[Ainley et al., 2005]
Decrease in sea ice extent	Later arrival and laying than in early 1950s / EA	9 seabird species	[Barbraud and Weimerskirch, 2006]
Warming, increased snowfall, decreased sea ice extent and duration	Alterations in phytoplankton and zooplankton community composition and changes in recruitment, abundance and availability of krill, replacement of Adélie by chinstrap peguins / WAP	Adelie, chinstrap penguins	[Ducklow et al., 2007]
Increased summer ice extent	Weaning masses decreased / RS	Weddell seal	[Proffitt et al., 2007]
Fine scale sea ice extent and local weather events	Chick abundances positively correlated with sea ice extent during July-September and large-impact ice anomalies suh as broke-off of iceberg B15A / WRS	Emperor penguins	[Barber-Meyer et al., 2008]
Monotonic shift pole-ward of krill due to sea ice extent decreasing	Prediction of spatial overlap due to shift of fin whales foraging range to higher latitudes where blue and minke whales used to feed / C	Whales	[Nicol et al., 2008]
Change in sea ice extent and timing	Ice-associated species such as blue and minke whales may be particularly affected, but to what extent is largely unknown / C	Whales	[Nicol et al., 2008]
Changes in the extent, persistence and type of sea ice	Prediction of negative effects on crabeater and Weddell seals; Ross and leopard seal, predicted to be the least negatively influenced; southern elephant and fur seals predicted to respond in ways opposite to the pack ice species ; for all alteration in food resources / WAP, RS	Crabeater, Weddell, Ross, leopard, elephant seals	[Siniff et al., 2008]
Lower-than-average fast ice extents and persistently short distances to nearest open water (foraging grounds)	Successful penguin breeding seasons / EA	Emperor penguins	[Massom et al., 2009]
Increase in polynya persitence overcome by decrease in pack ice thickness	Prediction of decrease of 50% of the colonies for 2025-2052 / C	Emperor penguins	[Ainley et al., 2010]
Increasing snowfall	Prediction of decrease of 75% of the colonies for 2025-2052 / C	Adélie penguins	[Ainley et al., 2010]
Decrease in the amount and extent of sea ice	Prediction of impact on crabeater and Weddell seals (hypothesis) / WAP	Crabeater, Weddell, elephant seals	[Costa et al., 2010]
Decrease in sea ice extent; increase in temperatures	Decrease in both populations, change in their main preys / WAP	Adélie, chinstrap penguins	[Trivelpiece et al., 2011]
Loss of sea ice and increasing krill fisheries	Reduction of food for pack ice seals, predited loss of seal habitat (1979-2011) / WAP, WWS	Crabeater, Weddell, leopard seals	[Forcada et al., 2012]
Absence of sea ice or heavy, persistent sea ice	Prediction of decline of the Adélie Land colony of 81% by the year 2100 / EA	Emperor penguins	[Jenouvrier et al., 2012]
Future and various sea ice changes over the circumpolar Antarctic sea ice	2/3 of the colonies are projeted to decline of at least 50%; Global population of at least 19% by 2100 / C	Emperor penguins	[Jenouvrier et al., 2014]
Increase of winter sea ice extent and duration, reduced spring-summer winds, increase of water colum stability favorable for phytoplancton	Years of positive chl-a associated with robust krill cohort the following summer, positive for penguins / WAP	Adélie penguins	[Saba et al., 2014]
Increase of winter sea ice duration between 1988 and 2011	Negative influence on female abundance in breeding colonies with a lag of three years, probably due to prevention of access to profitable prey patch areas / WRS	Elephant seals	[van den Hoff et al., 2014]
Climate-induced change in sea ice	Increase of population trend of emperor penguins over the past 75000 years, stable trend in the Weddell seal population; importance of intrinsic factors such as adaptative capabilities / EA	Emperor penguins, Weddell seals	[Younger et al., 2016]

Identifying how air-breathing marine predators take advantage of sea ice resources while tackling the constraint of this environment is a current challenge as:

- Our understanding of the complex linkages between sea ice and ecosystems still remains limited by restricted ship access, difficulties in sampling in remote environments during wintertime, and the patchiness of biota at any given location in the Antarctic sea ice zone [Brierley and Thomas, 2002, Steffens et al., 2006];

- The sea ice region is often regarded as a "frozen desert" [Flores, 2009] due to its low primary productivity in winter. However, food consumption of the top predator community persists or increases hundreds of kilometres deep into the pack ice; [Van Franeker et al., 1997, Flores et al., 2012b]. Past studies using pelagic sampling may have underestimated resources causing sea ice covered regions to appear poorer than they are in reality [Flores et al., 2012b];

- The complexity to estimating the cost of the physical constraint for marine predators due to the temporal lag between constraining areas and detectable responses in animal body condition, movements, breeding performance, survival for example.

In the present thesis, I attempted to overcome these limits. Indeed, the study of how environmental processes within the Antarctic sea ice zone shape species distribution in the vertical and horizontal dimension is a step towards the deepening of our knowledge on the functioning of the under-ice biological habitat and on the adaptation of marine predators to physical constraints in remote and extreme environments.

5 Context and objectives of the thesis

In the Southern Ocean, deep-diving predators moving across large scales, provide the opportunity to quantify how animals respond to different environmental conditions because their behavior and population dynamics are an integrated signal of dominant conditions within multiple marine habitats [Hindell et al., 2016]. Southern elephant seals in particular, are a useful model species to provide insights across broad geographic regions due to their circumpolar distribution, their long and distant migrations (they spend more than 10 months at-sea undertaking migrations that can extend several thousand kilometers) between sub-antarctic breeding colonies and foraging grounds within the Southern Ocean and their performance of long and deep dives (up to 2000 m) [Hindell et al., 1991b, McConnell et al., 1992, Hindell et al., 2016], see Figure I.17. During their two annual migration phases; postbreeding and postmoulting, they continuously dive [McIntyre et al., 2010a], and provide valuable information on the oceanographic conditions of their habitat [Charrassin et al., 2008, Roquet et al., 2013a, Roquet et al., 2014] through the use of miniaturised logging, satellite-linked monitoring equipment (see details in section

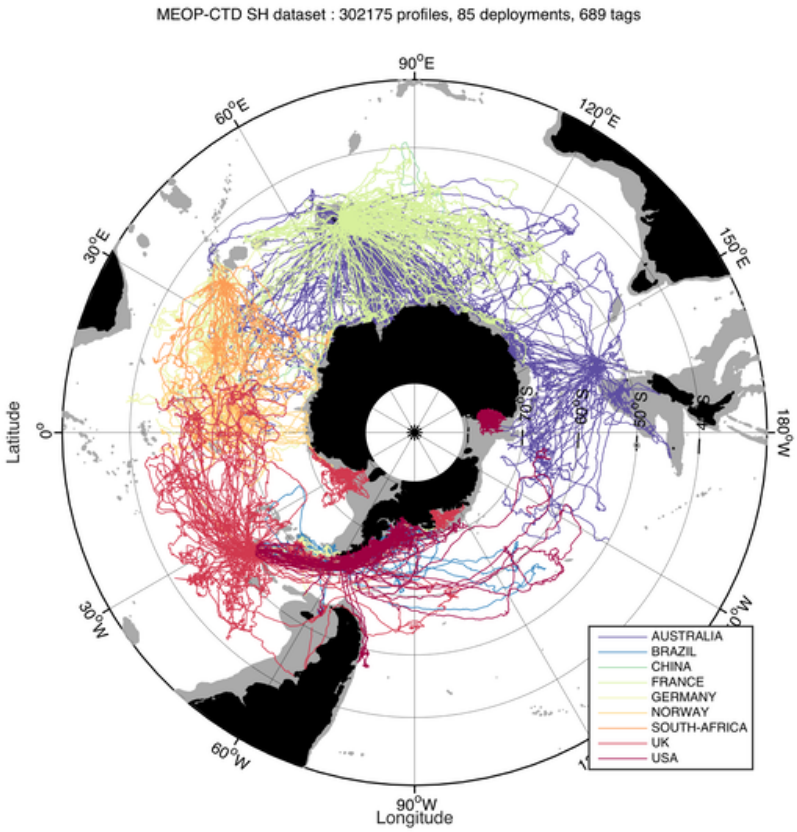


Figure I.17: Southern ocean map illustrating the distribution of CTD profiles from southern elephant and Weddell seals (i.e. vertical profiles of temperature and salinity) from the "Marine Mammals Exploring the Oceans Pole to Pole" (MEOP) database. This program brings together several national programmes to produce a comprehensive quality-controlled database of oceanographic data obtained in Polar Regions from instrumented marine mammals.

2.2, see Figure I.17). Central place foragers, southern elephant seals show strong site fidelity, returning reliably to natal breeding grounds twice a year, allowing for both attachment and recovery of telemetry instruments.

Southern elephant seals are distributed in four genetically distinct populations (see Figure I.18, [Slade et al., 1998, Hindell et al., 2016]): (i) The South Georgia in the South Altantic sector (~ 400,000 seals including South Georgia Island, South Orkney Island, South Shetland Island, Livingston Island, Elephant Island, Falkland Island, Gough Island, Bouvet Island), (ii) Peninsula Valdès (~ 56,000 seals), (iii) Kerguelen in the Southern Indian sector (~ 200,000 seals including Kerguelen Island, Heard Island, Marion Island, Prince Edward Island, Crozet and Possession I Islands), and (iv) Macquarie in the Southern Pacific sector (~ 60,000 seals including Macquarie Island, Antipodes Island, Campbell Island, Maatsuyker Island), see Figure I.18.

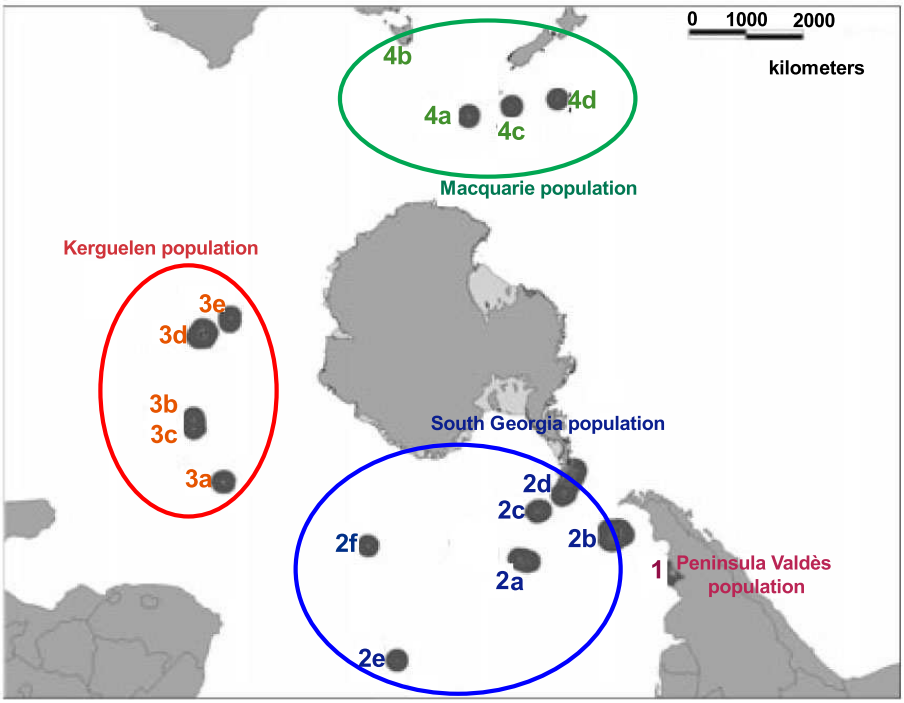


Figure I.18: Map of the circumpolar distribution of the four main population of southern elephant seals adapted from [McMahon et al., 2005, Hindell et al., 2016]. Numbers refer to: 1. Peninsula Valdès, 2. South Georgia (2a. South Georgia Island, 2b. Falkland Island, 2c. South Orkney Island, 2d. South Shetland Islands including Livingston Island and Elephant Island, 2e. Gough Island, 2f. Bouvet Island), 3. Kerguelen (3a. Prince Edward Islands including Marion Island, 3b and 3c. Crozet and Possession I Island, 3d. Kerguelen Island, 3e. Heard Island), 4. Macquarie (4a. Macquarie Island, 4b. Maatsuyker Island, 4c. Campbell Island, 4d. Antipodes Island).

Among the different populations, different demographic trends are observed: the population of Macquarie is following long-term and continuing declines; seals from the Kerguelen population declined in the recent past and have now stabilized; the population breeding on South Georgia has been stable for many decades; and the population of Peninsula Valdès is increasing [Hindell et al., 2016]. A number of hypothesis have been advanced to explain these different trends; the dominant explanation is that environmental conditions are different among the sectors of the Southern Ocean and among populations, modulating the availability of resources, principal factor of population growth [McMahon et al., 2005]. Indeed, variation in prey availability leads predators to use alternative foraging areas, modify foraging behaviour, which can affect their foraging performance, which in turn influences survival, breeding success and with a time lag population abundance [New et al., 2014]. Thus, foraging strategies will be different depending on the environmental conditions encountered and the regional contrasting trends in sea ice cover and dynamics observed in each sectors of the Southern Ocean.

In the present thesis, I will study the southern elephant seal population from Kerguelen (i.e. the one from Isles Kerguelen).

5.1 Comparison across southern elephant seal populations

The first objective is to understand the current stable demographic trend of the Kerguelen population by studying how environmental conditions modulate i) the availability of resources and ii) which in turn influences their foraging strategy, providing useful insights to compare among populations with contrasting trends. This objective will be tackled at the individual level, with a view informing the population level.

5.2 Strategies of the Kerguelen population

As detailed in section 3, southern elephant seals forage in two broad habitats: they either use the frontal regions of the ACC (over deep open water regions and the Kerguelen Plateau), or the Antarctic sea ice region comprising the shallow waters of the Antarctic shelf as foraging habitat. My thesis will describe the latter foraging strategy. Female southern elephant seals, like other capital breeders, depend on the energy gained and stored during their postmoult forging trip to feed their pups [Arnbom et al., 1993, Arnbom et al., 1997]. The energy intake during these foraging trips influences both pup mass at birth and at weaning and the subsequent survival of the pups in the first years of their life [McMahon et al., 2003, McMahon and Burton, 2005]. This early investment period has important consequences at the population level as juvenile survival can be an important determinant of population growth rates [McMahon et al., 2005]. Females foraging in Antarctic waters tend to wean larger pups than females foraging in the inter-frontal zone [Authier et al., 2012b] conferring a potential benefit in terms of pup survival. But this is a riskier strategy because inter-annual variability in sea ice may lead in some years to the presence of consolidated and constraining sea ice for breathing predators foraging in these areas. This has for consequences a higher energy expenditure compared to energy intake [van den Hoff et al., 2014]. It may be that the individual lifetime reproductive success of females employing the different strategies is the same, representing an evolutionary stable strategy. Foraging strategies of predators within the Antarctic sea ice are still poorly known due to the limited telemetry sensors that could be deployed over the 8 months post-moult trips, the limited ship access in this extreme environment (especially during winter), a reduced capability of satellite remote-sensing sytems due to cloud cover and the non-ability of Argos floats to work in ice [Costa et al., 2010]. **The second objective of the thesis aims to i) identify foraging strategies of Kerguelen southern elephant seals in the Antarctic sea ice region and ii) understand how environmental conditions in the Antarctic sea ice region makes this region profitable in terms of resources and prey availability compared to frontal areas.** This first objective is informing the population level, while the second objective zooms in, informing the subpopulation level.

5.3 Gender difference in foraging among the Kerguelen population

Finally, southern elephant seals utilize different habitats depending of their sex and age, for example the Kerguelen population shows two-distinct foraging strategies: 75% of the females forage in frontal areas of the ACC and 25% on the peri-Antarctic shelf while males forage on the Kerguelen and peri-Antarctic shelf [Bailleul et al., 2010a]. **The third objective of the thesis is to understand the difference between male and female strategies when seals foraged within the Antarctic sea ice region.**

5.4 Thesis outline

The thesis will be structured in four chapters, providing valuable information on the foraging strategies of Kerguelen male and female elephant seals in the Antarctic sea ice region to answer the three objectives outlined above. These chapters are:

- Chapter II: "*Winter use of sea ice and ocean water mass habitat by southern elephant seals: The length and breadth of the mystery*". This chapter investigates how combined hydrographic and sea ice conditions within the sea ice zone are linked to Kerguelen male and female elephant seal post-moult foraging strategies in winter.
- Chapter III: "*Under the sea ice: Exploring the relationship between sea ice and the foraging behaviour of southern 1 elephant seals in East Antarctica*". This chapter aims to identify gender-specific relationships between the post-moult foraging strategies of Kerguelen elephant seals in winter and spatio-temporal variability in sea ice concentration and coverage in East Antarctica. This chapter introduces the concept of constraints and benefits by describing how seal foraging activity is affected by the sea ice cover around its position in space and time and attempts to identify which type of sea ice environment would be constraining and/or beneficial for males and females.
- Chapter IV: "*Variability in sea ice cover and climate elicit sex specific responses in an Antarctic predator*".This chapter focusses on how the interannual variability of sea ice cover and dynamics influence the post-moult foraging behaviour of Kerguelen elephant seals in winter. In the context of climate change and variability, it is important to identify how medium term changes affect seal foraging strategy in order to understand how seal may adapt in the future. We propose mechanisms by which climate forcing affects both abiotic and biotic components of the Antarctic marine ecosystem, and in turn mesopredators through trophic cascading processes.
- Chapter V: "*Coastal polynyas: a winter oasis for top predators*". This chapter aims to identify the properties of a key winter habitat of male kerguelen elephant seals in winter, coastal polynyas and their influence on seal foraging activity. As noted previously, Antarctic coastal polynya ecosystem functionning is poorly known despite its high importance all year-round for a wide range of trophic levels. Studying its use by an apex predator is a step to fill this current gap.

6 Materials and methods

6.1 The southern elephant seal: a mesopredator of the Southern Ocean

Elephant seals belong to the suborder of Pinnipedia in the family Phocidae which includes 19 species distributed in 10 genera. The genus *Mirounga* includes the northern elephant seal (*Mirounga angustirostris*) breeding on the North American Pacific coast and the southern elephant seal (*Mirounga leonina*) inhabiting the Southern Ocean. The world population of southern elephant seals is estimated at ~ 749,000 individuals, and the subpopulation of Kerguelen Island (i.e. subpopulation 3d in Figure I.18) studied in the present thesis at ~ 150,000 [Hindell et al., 2016].

6.1.1 Biology

The reference for most of the section 6.1.1 is from [Hindell and Perrin, 2009].

Elephant seal's pronounced sexual dimorphism is one of the greatest of the animal Kingdom (see Figure I.19). Indeed, males are 3 to 4 times bigger than adult females. Males can weigh up to 4 tonnes and measure up to 6 m (on average 2 tonnes and 4 m respectively), in contrast females weigh on average 400 kg (between 300 and 800 kg) and measure 2.50 m. There are other marked sexual differences in morphology, all linked with the highly polygynous mating strategy of the species. One remarkable characteristic is the large proboscis of the male which plays a key role in dominance displays with other males (see Figure I.20). The sounds produced with the proboscis when the animal belch or roar are indicators of the mass of individuals and enable other males to acoustically measure the strength of the opposing male, in turn limiting fights.

Highly polygynous, large dominant males (beach masters) preside over large groups of aggregated females, known as harems. Competition between males for the top position is intense and leads to spectacular fights (see Figure I.21). Successful males will have almost exclusive access to harems consisting of up to 100 females, and so the reproductive success is high. This has led to the evolution of the marked proboscis and immense body size. Females reach sexual maturity between 3 and 5 years while males only reach it around 6-7 years but physical (or social) maturity only occurs around 10-11 years. Males manage to defend territories usually for one to three breeding seasons.

The annual breeding cycle begins when the largest males haul out on beaches in August. Pregnant females then haul out in large numbers, aggregating into harems, and giving birth to their single pup 2-5 days after arriving mainly in September-October. The females stay with their pups through the lactation period, never feeding and relying on their body-fat reserves. At birth, pups weigh 30-40 kg, and after 23-25 days, the duration of lactation, they weigh 120-130 kg. Mating starts several days before weaning. Although fertilization takes place at this time, the blastocyst does not implant until three months later. Once the pup is

Figure I.19: Illustration of the pronounced sexual dimorphism in southern elephant seals. Photo from Sara Labrousse at the site of Ratmanoff, Kerguelen Islands.

Figure I.20: Illustration of the large proboscis of the male southern elephant seal. Photo from Sara Labrousse at the site of Ratmanoff, Kerguelen Islands.

weaned, females have lost 40 to 50% of their mass and return to sea to feed, while the pups spend a further 4-6 weeks learning to swim and hunt relying heavily on their body large reserves of blubber, before going to sea.

Seals moult in February, leaving the sea to conserve body heat and the energy required to build the new skin and hair. Seals spend 3-5 weeks fasting during this period, relying again on their blubber reserves. At-sea their thermal insulation is assured by their large subcutaneous blubber, but this is less efficient during moult due the increased blood flow to the skin.

The annual cycle is represented in Figure I.22. **The present thesis focuses on the part of the annual cycle corresponding to the post-moult trips at-sea.**

Figure I.21: Illustration of the spectacular fights of male southern elephant seals. Photo from Sara Labrousse at the site of Ratmanoff, Kerguelen Islands.

Southern elephant seals spend 80% of their time at-sea, continuously diving to average depths of 500 m (but sometimes up to 2000 m) [McIntyre et al., 2010a, McIntyre et al., 2012] around 60 times per day and for 20-30 min (up to 90 min) [Hindell et al., 1991b]. As diving marine mammals, elephant seals must return repeatedly to the surface to breathe for in average 2 minutes, in total representing less than 2% of their time at-sea [Hindell et al., 1991b]. The size of elephant seal's eyes and their high concentration of pigments suitable for low-light vision and detection of bioluminescence indicate that vision plays an important role in the capture of prey in the darkness of great depth.

Southern elephant seals utilize radically different marine habitats between different sexes, ages, breeding colonies and according to individual preferences [Biuw et al., 2007]. Three main types of foraging habitats have been identified depending on sex and ages: adult males mostly use continental shelves (Antarctic shelf, Kerguelen Plateau or Campbell Plateau); while adult females and young males mostly exploit frontal systems of the ACC over deep basins or the marginal ice zone close to the Antarctic shelf [Bailleul et al., 2007a, Bailleul et al., 2010a, Authier et al., 2012a].

The longevity of southern elephant seals is 11-12 years for males (maximum is about 20 years), while it is 12-13 years for females (maximum of 25 years) ([Pistorius et al., 2000, Condit et al., 2014]. Their main predators are killer whales and southern sleeper sharks (*Somniosus antarcticus*).

Today, southern elephant seals are relatively free of negative interactions with humans, except when they are caught in fisheries nets. The effect of large-scale fisheries on preferred elephant seal prey species remains in question as it is difficult to quantify it given the incer-

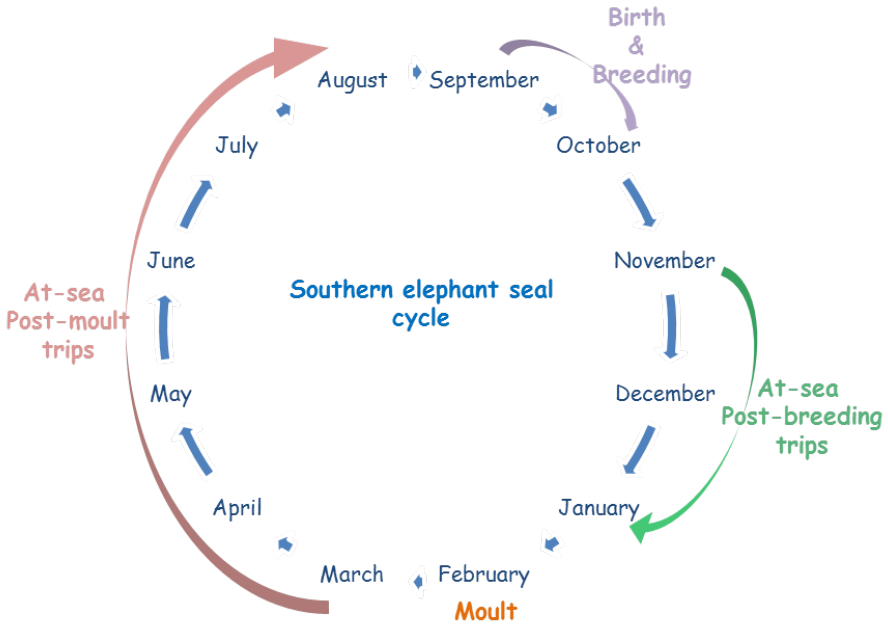


Figure I.22: Schematic representing the annual cycle of southern elephant seals. The cycle is composed by a breeding period in September-October on land, followed by a post-breeding trip at-sea from November to January, then animals moult in February and return at-sea for their long post-moult trip from March to August.

titude in elephant seal diet. However, this specie has a long history of direct exploitation by humans as seals were hunted extensively during the 1800s for their blubber giving a high-quality oil. The seal populations were reduced dramatically at all of their major breeding colonies. The exploitation continued until 1919 at Macquarie Island, 1964 at South Georgia and until 1953 at Kerguelen [Duhamel and Williams, 2011].

6.1.2 Diet

It is difficult to precisely define the different prey sources of southern elephant seals for the different regions as little is known about southern elephant seal prey and their latitudinal distribution. The diet of southern elephant seals is generally thought to be a mixture of fish and squid [Green and Burton, 1993, Daneri et al., 2000, Daneri, G.A. and Carlini, 2002, Bradshaw et al., 2003, van den Hoff et al., 2003, Cherel et al., 2008, Newland et al., 2009, Newland et al., 2011, Banks et al., 2014]. However, the relative proportion of each prey group consumed can vary considerably within and between populations, regionally, seasonally and between seals of different age and gender [Bradshaw et al., 2003, Field et al., 2004, Field et al., 2007b, Newland et al., 2009].

For males, there is an ontogenetic change in foraging ground selection from oceanic to neritic waters [Chaigne et al., 2013] and from small to large preys [Martin et al., 2011]. Thus, as they grow, southern elephant seal travel farther away and spend more time in

southerly regions [Field et al., 2004] and it has been suggested that adult males change their foraging strategy by consuming larger prey to meet their higher energetic requirements [Bailleul et al., 2010a, Martin et al., 2011].

A recent study coupling tracking data with fatty acid signature analysis (FASA) on female southern elephant seals from Macquarie Island, confirmed that diet varies spatially, with females using the shelf and pelagic habitats more likely to have higher proportions of fish in the diet and, while those from the pack-ice habitat were more likely to have a multi-species diet, i.e. a mixed diet of fish and squid [Banks et al., 2014]. [Bradshaw et al., 2003] using FASA from blubber of adult female southern elephant seals from Macquarie Island, suggested that the sub-adult and adult Notothenidae and Moridae are an important component of the winter diet.

By studying stomach lavaged on 153 southern elephant seals at King George Island, [Daneri, G.A. and Carlini, 2002] suggested that myctophid was the dominant fish family for off-shelf waters while in high Antarctic the Antarctic silverfish (Notothenidae) was dominating. This was completing the study of [Daneri et al., 2000] based on stomach lavages of 25 SES at King George Island who observed that Antarctic glacial squid *Psychroteuthis glacialis* was the predominant squid species. Finally, it has been shown that southern elephant seals also prey upon Antarctic toothfish [Brown et al., 1999].

6.2 Instrumentation

6.2.1 Description

In this thesis, animals were equipped with a head-mounted conductivity–temperature–depth satellite-relay data loggers (CTD-SRDLs, see Figure I.23, manufactured by the Sea Mammal Research Unit, University of Saint Andrews in Scotland).

This logger records dive depth and time every 4s, from which dive start time, dive end time, dive duration and post dive surface interval are determined. Only the four main inflection points of the time-depth time series, indicating a rapid change of the dive shape, are transmitted for each dive (see Figure I.24). The tag also measures hydrologic properties of the water column (conductivity, temperature) and pressure and transmits about 3 profiles per day (cf. Appendix A, Table AX2) corresponding with the ascent phase of the dives. The datapoints transmitted for each profile (mean of 16 ± 6 (SD), n = 29, cf. A, Table AX2) are a combination of temperature and salinity at a set of preselected standard depths, and at another set of depths chosen by a broken-stick algorithm that selects the important inflection points in temperature and salinity data (recorded every second during the ascent phase of the dives). All tags were initially calibrated at the laboratory and a part of them were also tested at sea against a ship based CTD before deployment. All tags were then post-calibrated using standardized procedures described in [Roquet et al., 2011, Roquet et al., 2014]. The minimum accuracies of post processed data were estimated to be at ± 0.03 °C in temperature and ± 0.05 psu, increasing to ± 0.01 °C and ± 0.02 psu in the best cases [Roquet et al., 2014].

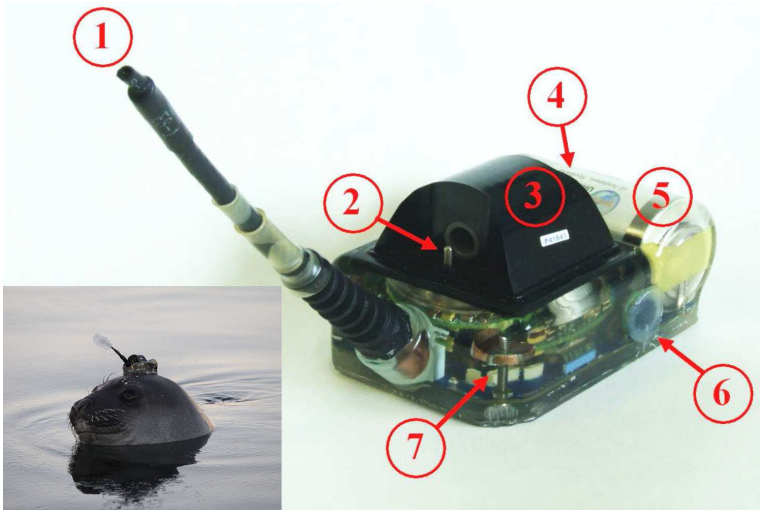


Figure I.23: Illustration representing the conductivity–temperature–depth satellite-relay data loggers and its characteristics from [Boehme et al., 2009]: 1. Antenna, 2; temperature sensor, 3. inductive cell for conductivity and in turn salinity, 4. pressure sensor (not visible), 5. battery, 6. communications port and 7. wet-dry sensor. Insert represents CTD-SRDL head-mounted on a southern elephant seal, photography from Clive McMahon.

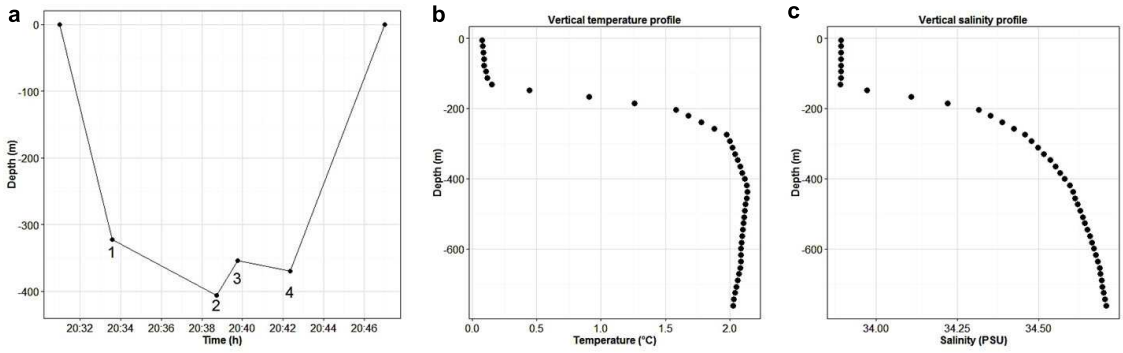


Figure I.24: Example of data recorded by CTD-SRDL for one dive. Panel a represents the dive profile with depth of the dive (expressed in meters) relative to the time of the dive (expressed in hours) associated with the four inflexion points. Panel b and c represents temperature/salinity profiles recorded during the ascent phase of dive, with depth of the dive (expressed in meters) relative to the temperature/salinity (expressed in °C/ psu).

Tag positions are estimated by the Argos system. When the seal surfaces, the tag emits at a known frequency short duration messages (of less than one second) to Argos instruments on satellites that pass overhead at an altitude of 850 km. The Argos satellites then calculate the location of the tag using the signal frequency drift (Doppler effect, [Argos, 2016]).

In this thesis, loggers recorded dive, temperature and salinity data over the whole post-moult trip of southern elephant seals, for at-sea durations of about 8 months (see Figure I.25).

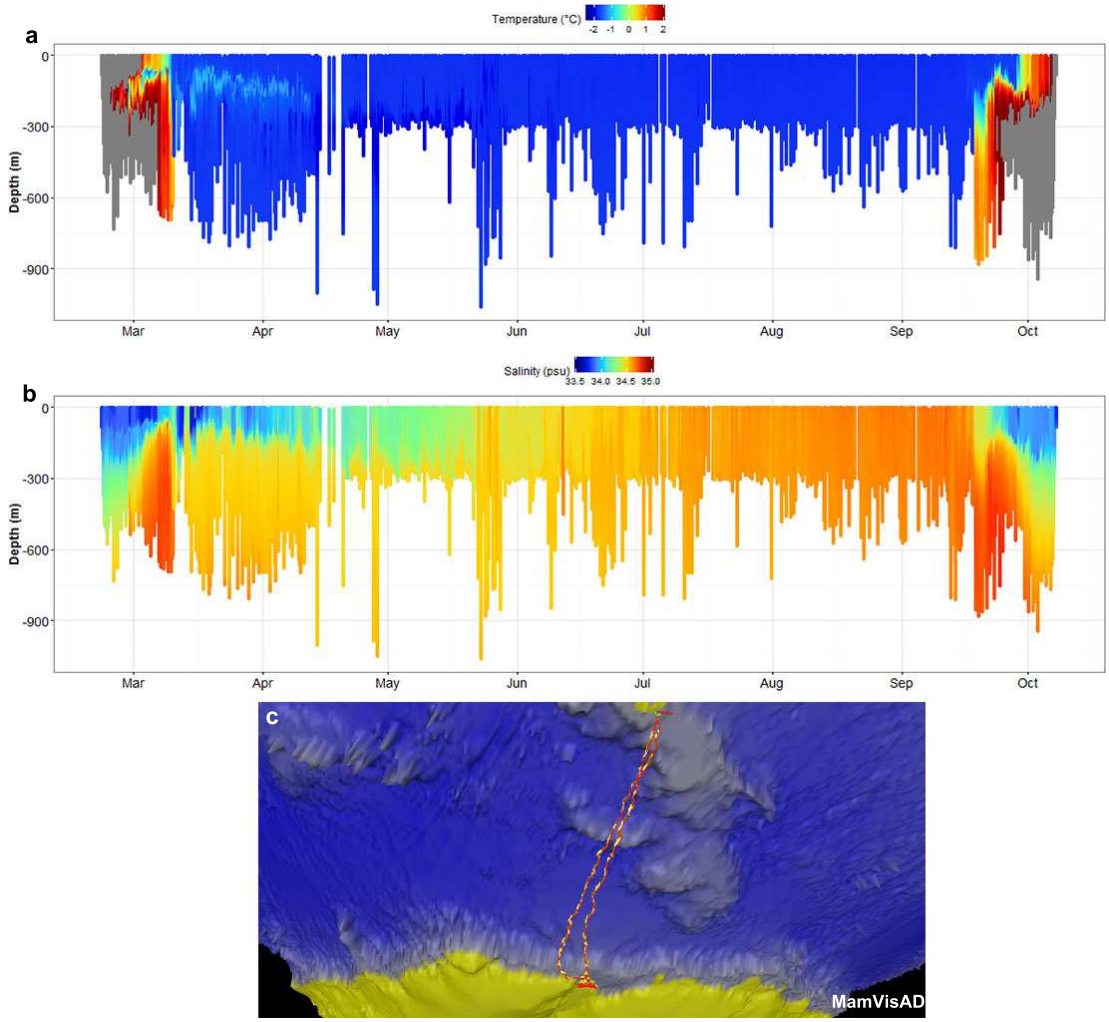


Figure I.25: Example of section of temperature and salinity data recorded during dives of the post-moult foraging trip of one seal in 2013 from March to October. Panel a and b represent the depth of dives (expressed in meters) relative to the time (expressed in months) and colours correspond to temperature (expressed in °C) / salinity (expressed in psu) respectively. Panel c represents the track of the seal during the whole trip based on Argos locations and created on MamVisAD, the background corresponds to the bottom topography.

For the purpose of chapter II, a dataset of 37 post-breeding female southern elephant seals from Kerguelen equipped with other types of loggers was used. However, these individuals were used to implement a model and do not belong to the primary dataset of this thesis. Thus, information about these will be found in the material and methods section of chapter II.

6.2.2 Datasets used in the study

A total of 46 post-moult southern elephant seals from Kerguelen Islands equipped between 2004 and 2014 were used in the present thesis (23 males and 23 females). For chapter II, 35 individuals were used (15 females and 20 males). For chapter III, 41 individuals were used (20 females and 21 males). For chapter IV, 43 individuals were used (21 females and 22 males). Finally, for chapter V, 23 males were used.

Details about which animals were used in each chapter, which animals visited the sea ice zone, and which animals had usable CTD data are detailed in the Table I.2.

6.2.3 Deployment and animal handling

Individuals were captured with a hooded bag (see Figure I.26, panel a, b) and anaesthetized using a 1:1 combination of tiletamine and zolazepam (Zoletil 100), which was injected intravenously [Field et al., 2002] with a dosage of 0.5 ml / 100 kg (see Figure I.26, panel c). Animals were weighed and measured (see Figure I.26, panel d) and data loggers were glued to the head of the seals using quick-setting epoxy (Araldite AW 2101, Ciba; [Field et al., 2012]; see Figure I.26, panel e).

6.2.4 Signal processing for analysis

Track data Locations estimated by Argos have varying uncertainty and often contain outliers. It is therefore necessary to process the position estimates using filtering methods. The quality of Argos locations depends mainly on the quality of the message sent by the tag and the number of satellites that have received this message. Each location is associated with a precision class (see Table I.3). This precision class is used by filtering methods to determine the error associated with the reconstructed animal's path.

I used state-space models (SSM) to filter all animal individual track location. SSM are a combination of a mechanistic model of individual movement, known as the process model, and an observation model (see Figure I.27, [Patterson et al., 2008]). The observation model gives the probability of getting a particular observation conditional on the animal's true position (i.e. its state). The state represents one or several variables, such as the animal's spatial location, and possibly a behavioural mode, such as foraging or migrating. The process model predicts the future state of an animal, given its current state (i.e. following the

Table I.2: Table summarizing the use of the 46 post-moulting southern elephant seals (23 females and 23 males) in each chapter. It includes ID, sex, year, if they visited sea ice, if CTD data were functional, and their use in each chapter. For chapter IV, SIA means that the individual was only used for the sea ice advance analysis; for chapter V, p means seals visited polynyas.

Individual	Sex	Year	Visit sea ice	CTD	Chapter II	Chapter III	Chapter IV	Chapter V
2004_1	M	2004	×	no	x	x	x	x
2004_2	M	2004	×	x	x	x	x	x, p
2004_3	F	2004	×	x	x	x	x	
2004_5	M	2004	×	x	x	x	x	x, p
2004_6	F	2004	×	x	x	x	x	
2004_7	F	2004	×	x	x	x	x	
2004_8	M	2004	×	x	x	x	x	x, p
2004_10	F	2004	×	x	x	x	x	
2008_1	M	2008	×	no	x	x	x	x, p
2008_2	F	2008	no	no	x		x, SIA	
2008_6	F	2008	×	no	x	x	x	
2008_7	F	2008	×	no	x	x	x	
2009_16	M	2009	×	x	x	x	x	x
2011_1	M	2011	no	x	x			x
2011_4	M	2011	×	x	x	x	x	x, p
2011_6	F	2011	×	x	x	x	x, SIA	
2011_7	M	2011	×	x	x	x	x	x, p
2011_9	M	2011	×	x	x	x	x	x, p
2011_10	F	2011	×		x	x	x	
2012_1	M	2012	×	x	x	x	x	x, p
2012_3	M	2012	×	x	x	x	x	x, p
2012_2	F	2012	×	no	x	x	x	
2013_1	F	2013	×	x	x	x	x	
2013_2	M	2013	×	x	x	x	x	x, p
2013_3	M	2013	×	x	x	x	x	x, p
2013_4	M	2013	×	x	x	x	x	x
2013_5	F	2013	×	x	x	x	x	
2013_7	F	2013	×	x	x	x	x	
2013_9	M	2013	×	x	x	x	x	x, p
2013_11	M	2013	×	x	x	x	x	x, p
2013_12	M	2013	×	x	x	x	x	x
2013_13	M	2013	×	x	x	x	x	x, p
2013_14	M	2013	×	x	x	x	x	x, p
2013_15	F	2013	×	x	x	x	x	
2013_18	F	2013	×	x	x	x	x	
2014_1	F	2014	no	non used				
2014_2	F	2014	×	non used		x	x	
2014_3	F	2014	×	non used		x	x	
2014_4	F	2014	no	non used			x, SIA	
2014_5	F	2014	no	non used				
2014_6	F	2014	×	non used		x	x	
2014_7	M	2014	×	x		x	x	x, p
2014_8	F	2014	×	non used		x	x	
2014_9	M	2014	×	x		x	x	x, p
2014_10	M	2014	×	x		x	x	x, p
2014_11	F	2014	×	non used		x	x	

Markov condition in mathematics). The observation model then weights these predictions by the likelihood of data, thereby linking the process model to the observations. Details on the software and package used are given in chapter II.

Table I.3: Table of class of precision for Argos localization from [Dragon, 2011].

Number of messages	Class of localization	Precision of localization (p)
≥ 4	3	p < 150 m
≥ 4	2	150 m ≤ p < 350 m
≥ 4	1	350 m ≤ p < 1000 m
≥ 4	0	p ≥ 1000 m
3	A	no estimation
2	B	no estimation
1	Z	no estimation

Dive data Errors were present in dive data recorded by CTD-SRDLs, such as outliers in dive depth and duration leading to dive data not biologically possible. These errors were removed and accounted for 3% of the total dataset (i.e. 8719 on 286843 dives). To overcome problems relative to surface depths between individuals, the start of the dive was considered when the depth exceeds the threshold of 15 meters. Below this threshold animals were considered at surface [Guinet et al., 2014].

Each dive was associated with a filtered Argos location using a time-based linear interpolation between the two Argos locations immediately preceding and following the dive. Dive metrics used were duration, bottom duration (time spent at greater than 80% of the maximum depth), maximum depth, ascent speed and descent speed (see Figure I.29). From track position, track turning angle (sinuosity) and horizontal speed (between two dives) were computed. Details about the method to define demersal from pelagic dives can be found in Appendix A, section A.

Finally, each dive was associated with a period of the day (day, night, twilight) considering its location and its start date time. To do this, solar angle was calculated for the time of each dive, using the R package *MapTools* (from R Development Core Team). Dives occurring during the night have a solar angle value ≤ −6°, dives during daylight have a solar angle value ≥ 0 and dives corresponding with twilight have a solar angle value comprised between −6° and 0.

6.3 Data analysis

6.3.1 Studying the foraging activity of a deep-diving wide-ranging predator: a current challenge

Understanding the effect of environmental variability on foraging behaviour requires knowledge of where and when animals feed and assimilate energetic reserves. A major challenge in marine ecology of top predators is the difficulty in obtaining appropriate foraging indices from simple behavioural data, particularly when distribution of prey is poorly known. In an environment where prey are patchily distributed, such as the open ocean, predators must continuously adjust their foraging behaviour according to the distribution and availability of their prey in order to maximize resource acquisition [Charnov, 1976, Fauchald and Erikstad, 2002]. Moreover, the energy expenditure associated with travelling from one patch of prey to another and then pursuing prey must be compensated with energy intake for the animal to remain in positive energy balance [MacArthur and Pianka, 1966]. Thus, one aspect of optimal foraging strategy suggests that predators will maximize the time spent in the vicinity of a successful prey patch by decreasing their displacement speed and increasing their turning frequency [Fauchald and Tveraa, 2003]. This behaviour, called "area restricted search" (ARS), is frequently observed in free ranging animals in the horizontal dimension (see Figure I.28). However, in the marine environment, resources are heterogeneous both in the horizontal and vertical dimensions. Therefore, we expect marine predators to adopt ARS behaviour not only along their track, but also while diving ([Heerah et al., 2014], see Figure I.28).

Most studies use proxies for feeding such as changes in vertical or horizontal movements, or time spent in specific areas (e.g. [Bailleul et al., 2007b, Bailleul et al., 2008, Biuw et al., 2007, Thums et al., 2011, Dragon et al., 2012a, Dragon et al., 2012b, Hindell et al., 2016]. On one hand, depending on the species and environmental conditions, inferring foraging success from horizontal tracking data only (i.e. surface locations) is not always possible, and could be misleading in identifying the true foraging activity that occurs at depth (e.g. [Weimerskirch et al., 2007]). This is particularly true in places where environmental conditions could constrain animal movements such as ice-covered areas [Bailleul et al., 2008] or when animals are resting [Sommerfeld et al., 2013]. In the case of a seal diving under heavy ice, sinuous and slow movements observed at the surface could lead to the identification of false ARS. On the other hand, vertical proxies such as maximum dive depth, dive duration, bottom time, descent/ascent rates and dive shape indices (see Figure I.29, e.g. [Dragon et al., 2012b]) can indicate areas where foraging effort is focused, they do not necessarily quantify the foraging success of the animal.

For different marine predators, foraging and prey capture are assumed to occur during the bottom phase of the dive, with predators spending a maximum time at depth (i.e. bottom time) and minimising transit time (i.e. descent and ascent phases) [Houston and Carbone, 1992, Thompson, 1993]. For different species, the bottom time was positively related to an index of foraging activity [Lesage et al., 1999, Watanabe et al., 2003,

Austin et al., 2006]. However, Dragon et al. [Dragon et al., 2012b] and Thums et al. [Thums et al., 2013] demonstrated that southern elephant seals foraging at deep depths had high descent / ascent rates, but relatively short bottom times. More importantly, when considering a sequence of dives from benthic divers, bottom duration was negatively correlated with foraging success (e.g. dive were shorter when feeding successfully), e.g. southern elephant seals [Bestley et al., 2014] or Australian fur seals [Foo et al., 2016]. In contrast, when considering only one dive from a pelagic diver, bottom duration were found to increase with foraging success at a given depth [Guinet et al., 2014]. This difference may be attributed to the type of habitat used: benthic prey occur in relatively low densities within a habitat, whereas mesopelagic prey tend to occur in higher-density patches, providing a richer food source once located. Therefore, it is likely that the relationship between foraging success and bottom duration varies with prey type and distribution, and the spatial and temporal scale at which it is investigated. A recent study on Weddell and southern elephant seals demonstrated that summarising the dive into three phases (consisting in descent, bottom and ascent) is overly simplistic. Indeed, increased foraging activity can occur several times during a dive and not necessarily or only during the bottom phase [Heerah et al., 2014]. Thus, using the bottom time as a single foraging index can be inaccurate. Finally, while the study of marine animal behavioural ecology has been considerably improved by the use of 3D accelerometers allowing to detect predator-prey interactions [Viviant et al., 2009, Viviant et al., 2014, Gallon et al., 2013, Guinet et al., 2014, Ydesen et al., 2014], this approach has been limited by the need to retrieve the tag where are stored the large quantity of high frequency acceleration data. Thus, this method is restricted to species for which the recovering of the tag was certain and it is still impossible to deploy accelerometers over the long winter trips of land-based species such as post-moult elephant seals.

Dive profiles are always transmitted in a highly summarised, low-resolution form (data from CTD-SRDLs, only the four main inflection points of the time-depth time series are transmitted, see Figure I.29, called hereafter "low resolution" dive profile), from which it is difficult to make the sort of behavioural inferences which are possible from higher-resolution datasets (such as detection of likely prey encounters). High resolution dive and accelerometry data (from time-depth recorder and accelerometer) correspond to a time-depth time series recorded every second, associated with 8-16 Hz acceleration data of the animal's head in 3 axes (longitudinal (surge), vertical (heave) and lateral (roll) axes).

My goal was to use a simple, but accurate tool to detect and quantify within-dive foraging periods in low-resolution dives. For this, we choose to use two different proxies of foraging activity:

- In chapter II, we first developed a new approach using indices of foraging derived from high resolution dive and accelerometry data to predict foraging behaviour in the extensive, low resolution dataset as developped by [Vacquié-Garcia et al., 2015], see Figure I.30 for details of this approach.

- In chapters III and IV, we used a metric developed by [Heerah et al., 2014, Heerah et al., 2015], the depth-based "hunting time", validated in a separate study where both depth and prey encounter events during the dives (as inferred from acceleration data) were available. This metric represents the total time spent in dive segments with decreased vertical velocity under a given threshold (0.4 $m.s^{-1}$) during which a large proportion of prey capture events (68% of all prey capture events inferred from acceleration data) have been shown to occur as part of the validation study [Heerah et al., 2015]. Furthermore, segments with hunting time were associated with four times more prey capture attempts than other segments. This index integrates the intensification of the foraging effort occurring several times within a dive and during descent, bottom and ascent phases. Thus, it is a meaningful index for both pelagic and benthic dives (see Figure I.31).

- For chapter V, both metrics were combined.

6.3.2 Characterization of the environmental habitat

The different environmental variables used in the present thesis are listed in table I.4.

Different analysis were performed to characterize the seal habitat. A short summary is presented below, while a complete description is available in each chapter:

- Extraction of ocean floor topography, sea ice concentrations, meridional winds at seal positions;

- Association of the closest CTD profile in time to each seal dive;

- Determination of the water masses at the bottom phase of dives;

- Extraction of the spatio-temporal variability of sea ice in a given radius around the seal positions;

- Computation of inter-annual sea ice concentration / meridional wind anomalies;

- The influence of environmental conditions on seal foraging activity was assessed using Linear Mixed effect Models (LMMs) or Generalised Linear Mixed effect Models (GLMMs);

- In Chapter IV, differences between negative and positive anomalies of sea ice parameters were assessed using a permutation test (bootstrap analysis).

6.4 East Antarctica: a laboratory for studying Antarctic ecosystems

The study site of the thesis is the East Antarctic region of the Southern Ocean (0–150°E).

Table I.4: Table of the different environmental data used in the thesis.

Type	Definition	Source
Bottom topography	GEBCO_08 Grid-database (30s per cell)	http://www.gebco.net/
Sea ice concentration, chapters II and III	Advanced Microwave Scanning Radiometer (AMSR-E) daily sea ice concentration images at 6.25 km resolution for years 2004–2011	http://www.iup.physik.uni-bremen.de:8084/amsr/amsre.html
Sea ice concentration, chapters II and III	Derived product from the Special Sensor Microwave Imager/Sounder (SSMI/S) satellite instrument of daily sea ice concentration images at 12.5 km resolution applied to a grid of 6.25 km for year 2012 created to fill the gap between AMSR-E and AMSR-2	http://www.iup.physik.uni-bremen.de:8084/amsr/amsre.html
Sea ice concentration, chapters II and III	AMSR-2 daily sea ice concentration images at 6.25 km resolution for years 2013, 2014	http://www.iup.physik.uni-bremen.de:8084/amsr/amsre.html
Surface winds for climatology and anomalies, chapter IV	Monthly ERA-Interim 10 m atmospheric reanalysis with a spatial resolution of approximately 80 km	http://apps.ecmwf.int/datasets/
Daily sea ice concentration for climatology and anomalies, chapter IV	Daily sea ice concentration from SSMI/S with a resolution of 25 km	NASA Earth Observing System Distributed Active Archive Center (DAAC) at the U.S. National Snow and Ice Data Center, University of Colorado, http://www.nsidc.org
Daily sea ice advance for climatology and anomalies, chapter IV	Calculated following [Massom et al., 2013] and using NASA Bootstrap SMMR-SSM/I NASA Team combined dataset of daily sea ice concentration with a resolution of 25 km	NASA Earth Observing System Distributed Active Archive Center (DAAC) at the U.S. National Snow and Ice Data Center, University of Colorado, http://www.nsidc.org
Sea ice production (SIP, $m.y^{-1}$) for polynyas definition, chapter V	SIP estimated by the heat flux calculation using the thin ice thickness data and surface atmospheric data. SIP calculation is performed twice a day over the entire Southern Ocean on the SSM/I Equal Area Scalable Earth-Grid (12.5 km) from 1992 to 2014	[Tamura and Ohshima, 2011]; thin ice thickness estimated from the algorithm developped in [Tamura et al., 2007]

The East Antarctic sea-ice zone has a strong seasonality with a large inter-annual variability characterised by significant mixed patterns from regional to local scales [Massom et al., 2013]. Globally, from 0 to 50°E, the winter sea ice cover has a large latitudinal range largely driven by net sea ice production within sea ice and at the sea ice edge [Kimura and Wakatsuchi, 2011b] and supplemented by an eastward transport of sea ice from strong westerlies (particularly during positive SAM events) [Deb et al., 2016] and within the eastern Weddell Gyre [Kimura and Wakatsuchi, 2011b]; (ii) from 50 to 90°E, the sea ice cover also extends far to the north, with a number of coastal polynyas producing large amounts of sea ice [Tamura et al., 2008] which is transported offshore by northward winds and the Prydz Bay Gyre, both within the climatological low-pressure Amery Bay region [Deb et al., 2016]; and (iii) from 90 to 150°E, a narrower zone of sea ice which is mostly fed by production in coastal polynyas and leads and supplemented by advection (input) from the east [Kimura and Wakatsuchi, 2011b, Massom et al., 2013]. Wind convergence (i.e. stronger northerly wind component during positive SAM events) in the eastern part can locally limit the sea ice extent resulting in compacting ice at the coast [Massom et al., 2008, Deb et al., 2016].

The intense westward flowing current along the Antarctic continental shelf break (the Antarctic Slope Current; ASC) is a dominant ocean circulation feature. The region from 30°E to 45°E is strongly influenced by the clockwise Weddell Gyre and region from 70°E to 80°E is influenced by the warmer, saltier and lower oxygen water transported close to the surface and the Prydz Bay Gyre (defined by a northward cyclonic recirculation of the ASC eastward of around 60-70 °E). From 80° to 150°E, [Bindoff et al., 2000] found that the continental shelf and slope regions have complex water-mass and frontal structures that vary with longitude. There is evidence of gradients in the ocean interior that suggest the presence of cyclonic eddies or meanders. The strong current along the slope and the large eastward flow in the western part of the region nearly form a closed gyre. This partial gyre, although much smaller in area size, is similar to the Weddell gyre found in the Weddell-Enderby Basin. These features represented in figure I.32 play an important role in the functioning of the peri-antarctic region, modifying its dynamic and thus resources available for the entire ecosystem from lower to higher trophic level.

Finally, [Arrigo et al., 2015] identified approximately twenty recurrent coastal polynyas around the East Antarctic coast (see Figure I.33). As detailed in the section 4.4.4, although the relationship between regional productivity and biomass at higher trophic levels in polynya regions is largely unknown, polynyas may be a critical component in the ecology of certain species [Massom et al., 1998].

The spatial heterogeneity of sea ice and ocean circulation feature in East Antarctica makes this region a valuable laboratory for our understanding of ecological processes taking place between top predators and the environment. We hypothesised and tested among the different chapters of this thesis that in East Antarctica:

- Complex sea ice patterns may dictate the distribution of prey species of apex predators (section 4.1 and 4.4);
- Complex regional circulation features such as the ASC [Bindoff et al., 2000] or upwelling of nutrient rich circumpolar deep water, onto the shelf [Jacobs, 1991] or discontinuities between nutrient-poor and nutrient-rich water masses [Prézelin et al., 2000] may result in increased biological activity which may control the distributions of apex predators;
- Polynya regions may be winter coastal oasis for apex predators.

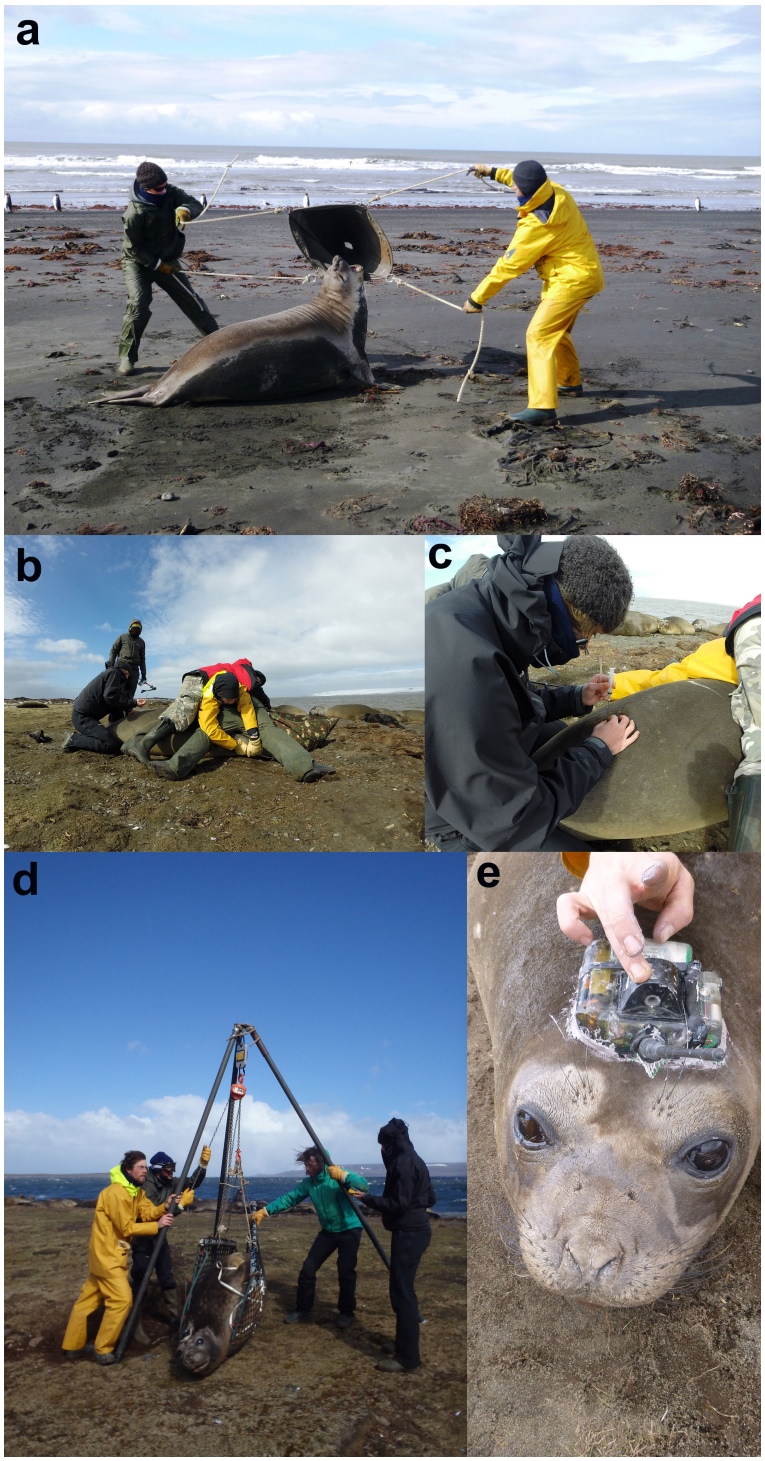


Figure I.26: Photographs illustrating animal handling and deployment in Kerguelen Islands, program IPEV 109. Panel a and b represent capture with the hooded bag and immobilization. Panel c represents sedation. Panel d represents weighing of the animal and panel e the tag glued on the seal head.

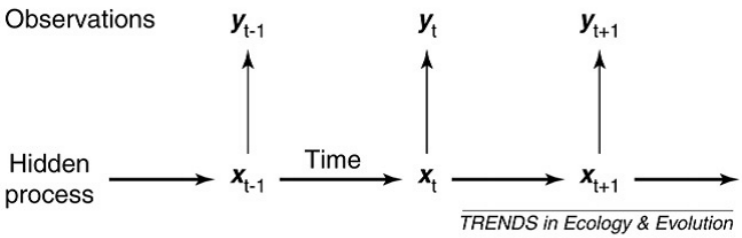


Figure I.27: General structure of the state-space model from [Patterson et al., 2008]. The *y*t are the data observed given the true, but unobserved, state *x*t. Horizontal arrows depict the process model prediction of the true state of the animal through time. Vertical arrows the observation model.

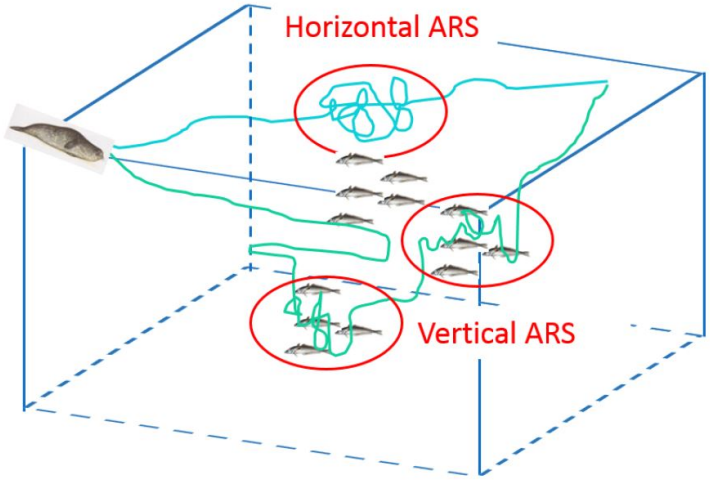


Figure I.28: Schematic of Area Restricted Search behaviour in the horizontal and vertical dimensions from [Heerah, 2014].

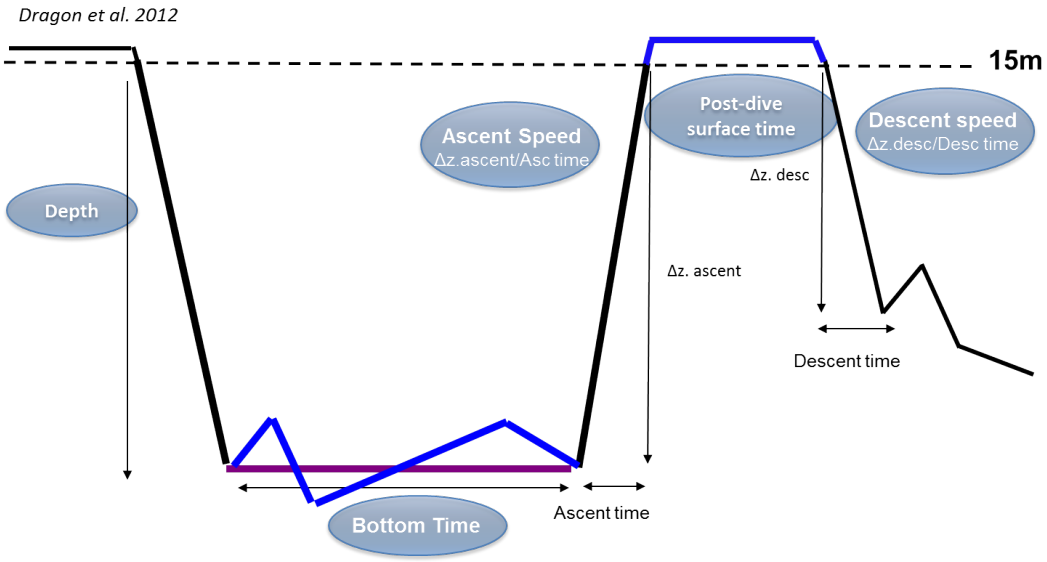


Figure I.29: Schematics of dive profiles and the dive metrics that can be calculated from it from [Dragon et al., 2012b].

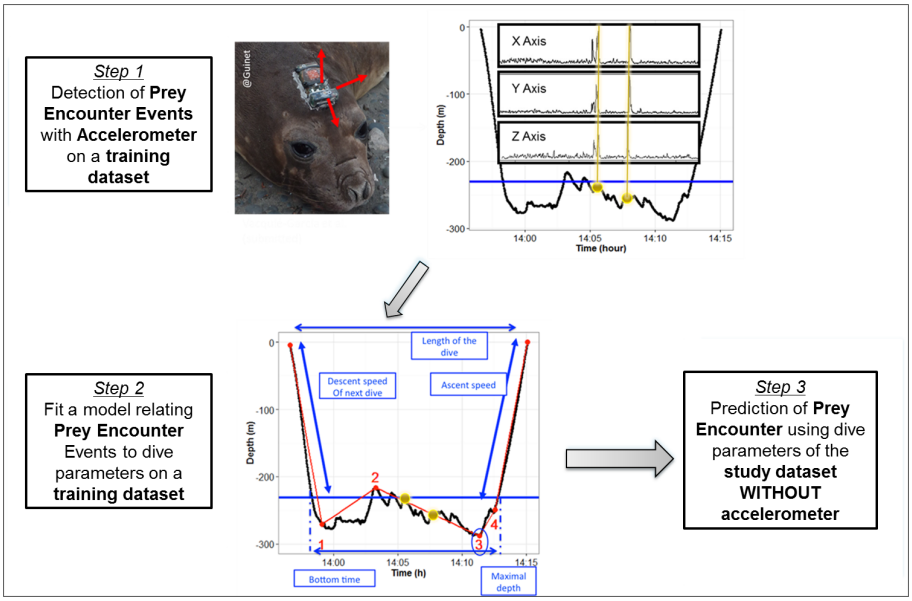


Figure I.30: Diagram summarizing the steps proceeded on the study dataset to compute the foraging index from the approach of [Vacquié-Garcia et al., 2015]. The first step consists in detecting on a training dataset of southern elephant seals equipped with accelerometers a significant acceleration on 3 axes likely corresponding with Prey Encounter Events (PEE). Then a predictive model was fitted relating PEE to dive parameters on this training dataset. The predictive model was then used to predict PEE on low resolution dive parameters of the training dataset without accelerometers.

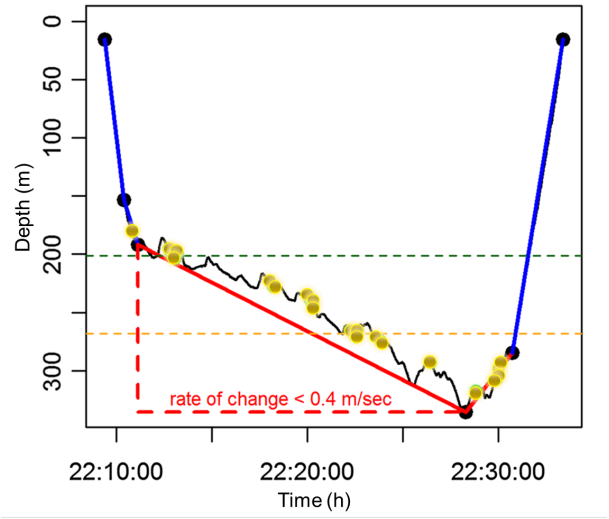


Figure I.31: Schematic describing segments of intensified foraging effort called "hunting time" derived from high resolution dive profiles and applied to low resolution dive profiles from [Heerah et al., 2015]. Both high-resolution dive profile and low resolution dive profile are represented. Red line represents "hunting time" mode (segment associated with vertical velocity 0.4 $m.s^1$ of low-resolution dive). Conversely, blue lines represent "transit" mode (segments associated with vertical velocity > 0.4 $m.s^1$ of low-resolution dive). Dotted lines represent the 80 (orange) and 60 % (green) of maximal dive depth. The yellow dots indicate prey encounter events (estimated from high-resolution acceleration data).

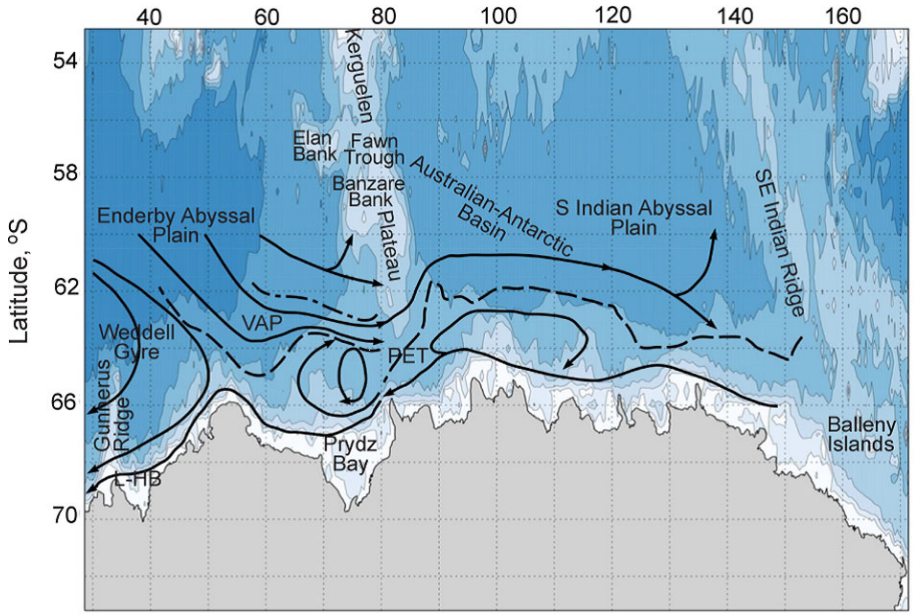


Figure I.32: Schematic from [Massom et al., 2013] representing large-scale ocean circulation patterns in the East Antarctic region (30-170°E) determined from hydrographic measurements (from [Nicol and Raymond, 2012]) superimposed on ocean bathymetry. The dashed lines indicate the location of the Southern Boundary of the ACC, and the dash-dotted line that of the Southern Antarctic Circumpolar Current Front, VAP Valdivia Abyssal Plain, and PET Princess Elizabeth Trough. Numbers along the x axes are degrees longitude east.

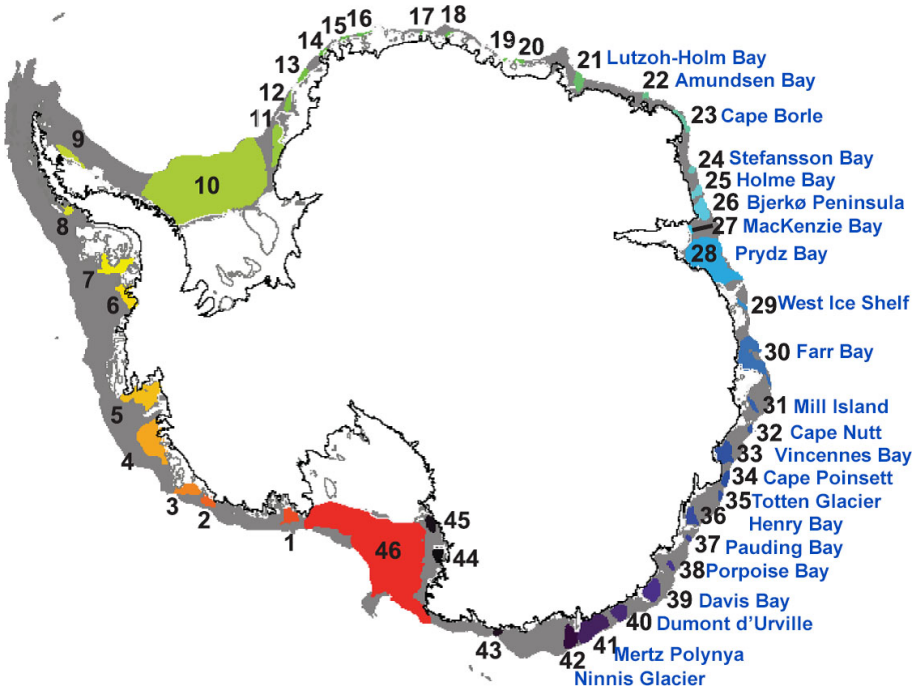


Figure I.33: Location of the 46 Antartic coastal polynyas from [Arrigo et al., 2015]. Names are given for the polynyas included in the study region of East Antarctica.

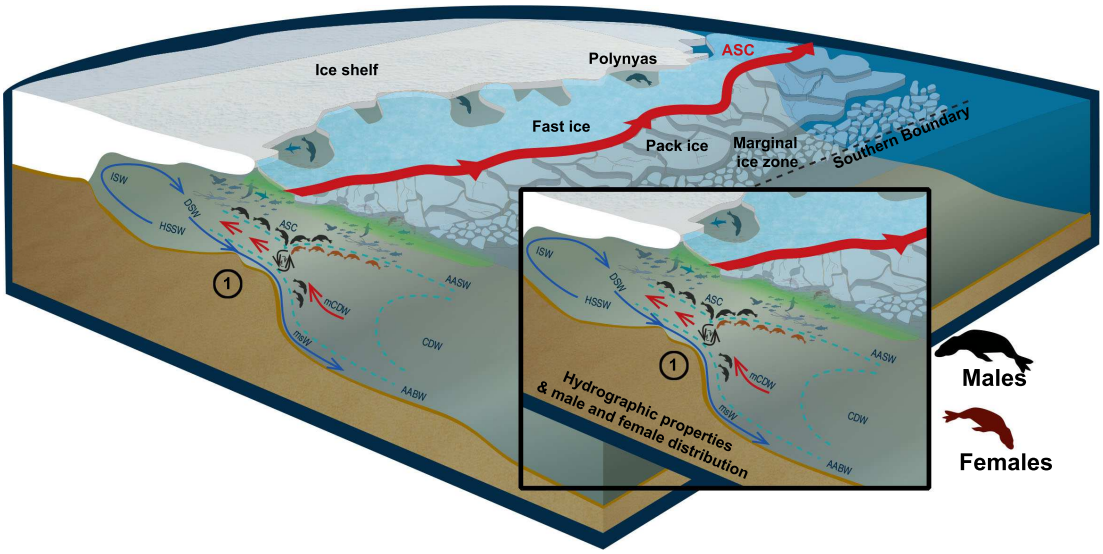
CHAPTER

II

Winter use of sea ice and ocean water mass habitat by southern elephant seals: the length and breadth of the mystery

This chapter has been published as *Winter use of sea ice and ocean water mass habitat by southern elephant seals: the length and breadth of the mystery* by S. Labrousse, J. Vacquié-Garcia, K. Heerah, C. Guinet, J-B. Sallée, M. Authier, B. Picard, F. Roquet, F. Bailleul, M. Hindell and J-B. Charrassin in ***Progress in Oceanography***, 2015. **DOI: 10.1016/j.pocean.2015.05.023**

Schematic of the results from chapter II. Refer to the general discussion 5 for detailed caption.



The aim of this first chapter was to examine the broad overview of the male and female foraging strategies within the Antarctic sea ice zone, expanding results of Bailleul et al. [Bailleul et al., 2007a] and combining together hydrographic and sea ice conditions parameters. This was a basis for the development of the following chapters. The general foraging strategies and movements patterns of male and female within the sea ice zone were identified.

Highlights

- Time-series of 35 elephant seal winter foraging trips to Antarctica were analyzed
- A high resolution dive behaviour dataset was used to predict foraging events
- The links between foraging and sea ice, hydrography and topography were quantified
- Foraging strategies depended on the sex of seals
- The foraging activity was associated with a number of oceanographic discontinuities

Abstract

Understanding the responses of animals to the environment is crucial for identifying critical foraging habitat. Elephant seals (*Mirounga leonina*) from the Kerguelen Islands (49°20'S, 70°20'E) have several different foraging strategies. Why some individuals undertake long trips to the Antarctic continent while others utilize the relatively close frontal zones is poorly understood. Here, we investigate how physical properties within the sea ice zone are linked to foraging activities of southern elephant seals (SES). To do this, we first developed a new approach using indices of foraging derived from high temporal resolution dive and accelerometry data to predict foraging behaviour in an extensive, low resolution dataset from CTD-Satellite Relay Data Loggers (CTD-SRDLs). A sample of 37 post-breeding SES females were used to construct a predictive model applied to demersal and pelagic dive strategies relating prey encounter events (PEE) to dive parameters (dive duration, bottom duration, hunting-time, maximum depth, ascent speed, descent speed, sinuosity, and horizontal speed) for each strategy. We applied these models to a second sample of 35 seals, 20 males and 15 females, during the post-moult foraging trip to the Antarctic continental shelf between 2004 and 2013, which did not have fine-scale behavioural data. The females were widely distributed with important foraging activity south of the Southern Boundary Front, while males predominately travelled to the south-eastern part of the East Antarctica region. Combining our predictions of PEE with environmental features (sea ice concentration, water masses at the bottom phase of dives, bathymetry and slope index) we found higher foraging activity for females over shallower seabed depths and at the boundary between the overlying Antarctic Surface Water (AASW) and the underlying Modified Circumpolar

Deep Water (MCDW). Increased biological activity associated with the upper boundary of MCDW, may provide overwintering areas for SES prey. Male foraging activity was strongly associated with pelagic dives within the Antarctic Slope Front where upwelling of nutrient rich Circumpolar Deep Water onto surface water may enhance and concentrate resources. A positive association between sea ice and foraging activity was found for both sexes where increased biological activity may sustain an under-ice ecosystem. Variability of the East Antarctic sea ice season duration is likely a crucial element to allow air-breathing predators to benefit from profitable prey patches within the pack ice habitat.

1 Introduction

The Southern Ocean is highly productive which influences the structure and dynamics of the Antarctic marine ecosystem at all trophic levels [Tynan, 1998, Nicol et al., 2000b, Nicol et al., 2000a]. Short and intense phytoplankton blooms [Smetacek and Nicol, 2005] are dependent on spatio-temporal distribution of nutrients, themselves determined by interactions between topography of the seafloor, water mass properties and circulation, ocean currents and sea ice seasonality [Prézelin et al., 2000, Brierley and Thomas, 2002]. The continental shelf, polynyas, sea ice edge and areas where the bathymetric profile allows intrusion of nutrient rich water masses onto the shelf (such as Circumpolar Deep Waters) stimulate primary productivity [Moore and Abott, 2000, Nicol et al., 2005] and the population growth of mid [Prézelin et al., 2000] and upper trophic levels [La Mesa et al., 2010] including top predators. The latter includes purely Antarctic species and also species breeding in the sub-Antarctic, such as southern elephant seals (SES, *Mirounga leonina*, [Biuw et al., 2007, Biuw et al., 2010]), king penguins (*Aptenodytes patagonicus*, [Bost et al., 2004]) and Antarctic fur seals (*Arctocephalus gazella*, [Arthur et al., 2016]). However, the nature of the linkages between environmental factors and higher trophic levels is unclear.

In this study, we investigated how physical environmental factors influence SES foraging strategies in the East Antarctic region of the Southern Ocean (0–150°E). This region is characterized by considerable intra- and inter-annual variation in sea ice and prominent ocean circulation features including the eastern end of the Weddell gyre, and an intense westward flowing current steered by the Antarctic continental shelf (the Antarctic Slope Current; ASC). Reported changes and variability in sea ice and ocean water masses in the East Antarctic region are possibly associated with changes in ocean circulation patterns (e.g. [Rintoul, 2007, Nicol and Raymond, 2012, Massom et al., 2013]). These changes can be rapid and complex with contrasting signals in close areas on regional to local scales. However, how these local changes of the environment would influence the dynamics of the entire ecosystem is poorly understood.

Several hypotheses have been proposed to link local environmental factors with apex predator foraging behaviour. One is that sea ice variability in East Antarctica may dictate the distribution of prey species, many of which are known to interact with

sea ice. For example, krill (*Euphausia superba*) living within the seasonal pack ice zone depends on ice-algae to survive in winter (e.g. [Daly, 1990, Atkinson et al., 2004, Meiners et al., 2012]) and mesopelagic fish such as the Antarctic lanternfish (*Electrona antarctica*) feed on krill and other zooplankton under pack ice [Kaufmann et al., 1995]. A second hypothesis is that discontinuities between nutrient-poor and nutrient-rich water masses may result in increased biological activity at these water masses boundaries [Rodhouse and Clarke, 1985, Prézelin et al., 2000], providing rich food sources that could be easily detected [Sticken and Dehnhardt, 2000] and exploited by predators [Boyd and Arnbom, 1991]. A third hypothesis is that the complex regional circulation features such as the Antarctic Slope Front (ASF) may control the distributions of chlorophyll, krill and apex predators [Bindoff et al., 2000]. This would be largely due to upwelling of nutrient rich circumpolar deep water, onto the eutrophic zone on the shelf, which would enhance productivity [Jacobs, 1991].

Elephant seals are deep-diving, wide-ranging [Hindell et al., 1991a, Hindell et al., 1991b, McConnell et al., 1992] top predators of the Southern Ocean that utilize radically different marine habitats between different sexes, ages, breeding colonies and according to individual preferences [Biuw et al., 2007]. The main populations are located in the South Atlantic, Southern Indian, and South Pacific oceans, and display contrasting demographic trends, presumably in response to environmental variability [McMahon et al., 2005]. SES from Kerguelen show two-distinct foraging strategies: 75% of the females forage in frontal areas of the Antarctic Circumpolar Current (ACC) and 25% on the peri-Antarctic shelf. Males forage on the Kerguelen and peri-Antarctic shelf [Bailleul et al., 2010a]. Our understanding of the foraging behaviour of SES and its interplay with environmental features such as hydrography, sea ice, bottom topography or dynamic environmental features such as eddies and fronts has increased in recent years [Bornemann et al., 2000, Bailleul et al., 2007a, Bailleul et al., 2007b, Bailleul et al., 2010a, Bailleul et al., 2010b, Biuw et al., 2007, Biuw et al., 2010, Bestley et al., 2012, Guinet et al., 2014, Hindell et al., 2016]. However, no studies on Kerguelen SES have quantified the role of combined environmental factors that would make migrations of male and female within the East Antarctic sea ice zone during winter profitable and sustainable over years. Unique environmental features and important life history stages may hold the answer to the causes underpinning seal movements.

Understanding the effect of environmental variability on foraging behaviour requires knowledge of where and when animals feed and assimilate energetic reserves. A major challenge in marine ecology of top predators is the difficulty in obtaining appropriate foraging indices from simple behavioural data, particularly in the context of poorly known prey fields. Most studies use proxies for feeding such as changes in vertical or horizontal movements, or time spent in specific areas [Bailleul et al., 2007b, Bailleul et al., 2008, Biuw et al., 2007, Thums et al., 2011, Dragon et al., 2012a, Dragon et al., 2012b, Hindell et al., 2016]. Although these proxies can

indicate areas where foraging effort is focused, they do not necessarily quantify the foraging success of the animal. New approaches employing acquisition of high resolution data of seal body dynamics from accelerometers are now filling the gap [Guinet et al., 2014].

By simultaneously recording animal location, dive behaviour and hydrographic profiles in situ and in real time, we studied the foraging behaviour of Kerguelen elephant seals migrating during post-moult movements from the Kerguelen Islands to the Antarctic shelf. The aim of the study was to identify and quantify the role of environmental features involved in the acquisition of food resources for SES during winter trips in the Antarctic sea ice zone. We developed a new approach using indices of foraging derived from high resolution dive and accelerometry data (prey encounter events, PEE) to predict foraging behaviour in an extensive, low resolution dataset from CTD-Satellite Relay Data Loggers (CTD-SRDLs). Information on the properties of water masses, sea ice concentration and topography was combined and sexual differences were investigated.

2 Materials and methods

2.1 Animal handling and tag deployment

Two different datasets were used in this study; one as a training dataset to build a predictive model of foraging behaviour (hereafter, referred to as the training dataset), and a second on which that model was used to predict foraging in space and time and relate foraging activity to environmental features of the region (referred to as the study dataset). A summary of the different steps followed in this study is presented in Figure II.1.

The training dataset consisted of 37 post-breeding SES females captured on the Kerguelen Islands (49°20'S, 70°20'E) in October/November between 2008 and 2013 (Appendix A, Table AX1). Twenty three seals were equipped with a head-mounted GPS capable of relaying data via satellite using Service Argos combined with an archival data logger (SPLASH10-Fast-Loc GPS, Wildlife Computers; WC). SPLASH10 devices transmitted Argos location data, collected GPS location data at 20 min intervals and recorded pressure at 1 or 2s intervals. In addition, 12 seals were equipped with a head-mounted conduc tivity–temperature–depth satellite-relay data loggers (CTD-SRDLs, Sea Mammal Research Unit, University of St Andrews), and 2 others with Smart Position and Temperature Tags (SPOT, WC). All tags were combined with a TDR-accelerometer data logger (MK10-X, Wildlife Computers), sampling acceleration and pressure. Acceleration was measured at 16 Hz on 3 axes (longitudinal (surge), vertical (heave) and lateral (roll) axes) and the separation between dynamic and gravitational acceleration was done via post-processing of all 3 axes.

The study dataset consisted of 35 post-moulting SES, 20 males and 15 females, that were captured on the Kerguelen Islands between December/February from 2004 to 2013 (Appendix A, Table AX2). For this analysis we used only post-moulting SES that used the sea ice zone. All animals were equipped with CTD-SRDLs (Sea Mammal Research Unit,

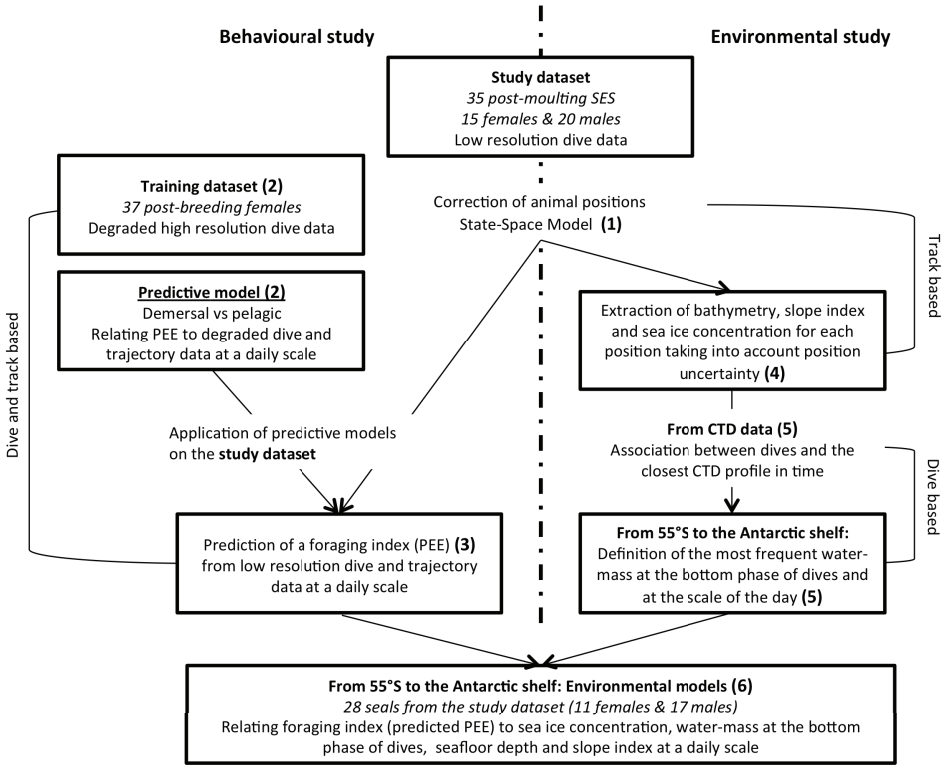


Figure II.1: Diagram summarizing the different steps of both behavioural and environmental studies. Numbers refer to the order in which these steps were realized.

University of St Andrews) measuring conductivity, temperature and pressure. An average of 2.8 ± 1 CTD profiles (n = 29) were transmitted daily [Boehme et al., 2009] and the tag positions were estimated by the Argos system. For all CTD-SRDLs (from Sea Mammal Research Unit, University of Saint Andrews), the datapoints transmitted for each profile (mean of 16 ± 6 (SD), n = 29) are a combination of T (temperature) and S (salinity) at a set of preselected standard depths, and at another set of depths chosen by a broken-stick algorithm that selects the important inflection points in T and S data (recorded every second during the ascent phase of the dives). All tags were initially calibrated at the laboratory and a part of them were also tested at sea against a ship based CTD before deployment. All tags were then post-calibrated using standardized procedures described in Roquet et al. [Roquet et al., 2011, Roquet et al., 2014]. The minimum accuracies of post processed data were estimated to be at ±0.03°C in temperature and ± 0.05 psu, increasing to ± 0.01°C and ± 0.02 psu in the best cases [Roquet et al., 2014].

Individuals were anaesthetized using a 1:1 combination of tiletamine and zolazepam (Zoletil 100), which was injected intravenously [Field et al., 2002]. Data loggers were glued to the head of the seals using quick-setting epoxy (Araldite AW 2101, Ciba; [Field et al., 2002]). Instruments were retrieved from post-breeding females upon returning from their foraging trip.

Females in the training dataset had an average weight of 288 ± 51 kg (mean ± standard deviation) and an average length of 243 ± 14 cm, similar to the weight and length of females from the study dataset of 324 ± 56 kg and 244 ± 16 cm respectively. However, males were heavier and longer than females (553 ± 256 kg and 292 ± 41 cm).

2.2 Behavioural data

2.2.1 Filtering trajectories

Of the 37 females in the training dataset, 23 individuals provided GPS positions, while 14 had only Argos locations. For both types, a simple speed filter similar to McConnel et al. [McConnell et al., 1992] was used.

For 35 individuals of the study dataset, Argos positions were filtered using State-Space-Model (SSM) (step 1, Figure II.1) with the package *bsam* following Jonsen et al. [Jonsen et al., 2013]. Locations of class Z (i.e. the lowest location quality index provided by Service Argos, and for which no stated position uncertainty is provided) were removed prior to analysis. Two Markov chains with a total of 100,000 simulations were computed, taking one in ten samples, with a burn in of 50,000 simulations. The analysis sets an interval of 6 h between each position and for each position we obtained 5000 samples per chain. The average of the 10,000 samples gave the estimated position of the animal as well as uncertainty estimate associated with this position. Confirmation of the convergence of the model was checked graphically. Two individuals were removed from analysis due to devices functioning for less than 30 days. Each dive's location was based on a time-based linear interpolation between corrected locations.

2.2.2 Dive data collected

For the training dataset, data from accelerometers were processed according to Viviant et al. [Viviant et al., 2009] and Gallon et al. [Gallon et al., 2013]. Identification of prey encounter events (hereafter PEE) from the accelerometry data followed Guinet et al. [Guinet et al., 2014]. A PEE does not mean that the seal was necessarily ingesting food, but should be considered as an index of prey encounters during the dive.

For the study dataset, tags were programmed to record dive depth and time every 4s, from which dive start time, dive end time, dive duration and post dive surface interval were determined. Only the four main inflection points of the time-depth time series, indicating a rapid change of the dive shape, were transmitted for each dive according to tag programming (Sea Mammal Research Unit).

For both datasets, a zero offset surface correction was set to 15 m [Guinet et al., 2014]. Only dives deeper than 40 m and longer than 3 min were kept for analysis.

2.2.3 Predictive model of foraging behaviour

Following Viviant et al. [Viviant et al., 2014], we developed indices of foraging derived from high resolution dives, trajectory and PEE to estimate foraging behaviour from the lower temporal resolution dataset (CTD-SRDLs). The purpose of this step was to first use the high resolution training dataset to identify dive and trajectory parameters associated with high PEE (step 2 of Figure II.1). Using these results we then calculated PEE per day based on diving and movement patterns of the 35 individuals equipped with CTD-SRDLs (study dataset; step 3 of Figure II.1) for which no information on foraging success was available otherwise.

To obtain dive profiles with a similar resolution for both the training dataset used to construct the model (37 post-breeding SES) and the study dataset used to apply the prediction (35 post-moulting SES), we first computed a "broken-stick" algorithm (from Heerah et al. [Heerah et al., 2014]) to degrade high resolution dive data into the four inflection time-depth points, i.e. identical to the dive data provided by the CTD-SRDLs. The variables (from degraded dive data) used to describe foraging behaviour were dive duration, bottom duration (time spent at 80% of the maximum depth), hunting-time (see [Heerah et al., 2014]), maximum depth, ascent speed, descent speed of the next dive, track turning angle (sinuosity) and horizontal speed (between two dives). These values were averaged for each day because the predictive abilities of similar models were low at the scale of a single dive and higher at a scale of a day containing multiple dives [Viviant et al., 2014]. The daily PEE was calculated from the rate of PEE per hour multiplied by 24 h.

Southern elephant seals display either a demersal or pelagic foraging strategy (i.e. the dominant type of dive behaviour in a given day) depending on the habitat [Bailleul et al., 2007a, Bailleul et al., 2007b], which might influence patterns of foraging activity and dive behaviour. Therefore, to build the model, the training dataset was divided into pelagic and demersal dive strategies for locations on the Kerguelen shelf (Appendix A, section A).

We then used a generalized linear mixed model (GLMM) to identify the most informative variables explaining daily PEE for each strategy based on the training dataset (Appendix A, section A). A quasi-Poisson distribution was used for the error structure of the response variable and individuals were included as random factor. When applying the models to the study dataset, we distinguished between demersal and pelagic strategy over the peri-Antarctic shelf (rather than the Kerguelen Shelf) (Appendix A, section A). The statistical model (averaged regression coefficients obtained from model averaging) was then applied to the variables of the study dataset for each strategy to predict PEE per day for the 35 post-moulting individuals (step 3 of Figure II.1; Appendix A, section A).

2.3 In situ and remotely sensed oceanographic data

2.3.1 In situ salinity and temperature profiles

Among the 35 study individuals, 29 had usable CTD (Conductivity–Temperature–Depth) profiles. To obtain continuous T and S vertical profiles, a linear interpolation with a vertical resolution of 18 m was applied. The resolution of 18 m was chosen as the best compromise between high vertical resolution and avoiding addition of non-available data or loss of information [Heerah et al., 2013]; the minimum of the mean intervals (for each individual) between two data points for all profiles was 18.3 m). CTD positions were corrected by interpolating SSM locations along the track based on the CTD date and time. Water masses sampled during the transit of seals along their trip from 55°S to the Antarctic continent were then determined from their temperature, salinity and neutral density γn [Jackett, D.R., McDougall, 1997]. We distinguished between nine water masses [Bindoff et al., 2000, Meijers et al., 2010]: (1) Intermediate Water (IW); (2) Antarctic Surface Water (AASW); (3 and 4) Modified and Circumpolar Deep Water (CDW, MCDW); (5) High Salinity Modified Circumpolar Deep Water (HSMCDW); (6) Mixed Shelf Water (MSW); (7) Antarctic Bottom Water (AABW); (8) High Salinity Shelf Water (HSSW); and (9) Ice Shelf Water (ISW). Criteria to define these water masses were adapted from [Bindoff et al., 2000, Meijers et al., 2010, Lacarra et al., 2011, Orsi, 1995], and are presented in Table II.1.

To identify the water mass used when the seals were foraging, we used the water mass encountered during the bottom phase of each dive, as this is where most PEE are expected to occur [Guinet et al., 2014] (step 5 of Figure II.1). Each dive was then associated with the closest CTD profile in time collected by the same individual (step 5 of Figure II.1). A maximum time interval of 12 h between the CTD and the dive was set, leading to an average distance difference between the CTD and the dive of 9.1 ± 9.6 km. Following this procedure, 70.4% of dives were associated with a CTD profile.

2.3.2 Extraction of ocean floor topography and sea ice concentrations at animal positions

This study focused on individuals using the Antarctic shelf and the sea ice zone. The maximum extension of sea ice was reached in September at latitudes close to 55°S. The area south of 55°S to the Antarctic continent was used as the spatial domain for the environmental study where hydrology, topography and sea ice data were linked to foraging behaviour.

Two bathymetry datasets were used; the GEBCO One Minute Grid-database (10 per cell grid) for graphical purpose, and GEBCO_08 Grid-database (30s per cell) for analysis (http://www.gebco.net/).

To take into account the spatial error associated with each location when extracting environmental variable under the seals' tracks, the mean and variance/covariance matrix of the 10,000 posterior samples available after the filtering process for each position es-

Table II.1: Definition criterions of water masses determined from CTD-SRDLs temperature, salinity, pressure collected by the 29 post-moulting seals at the bottom phase of dives from 2004 to 2013 along tracks from 55°S to the Antarctic continent and from 0 to 150°E.

Abbreviation	Type of water mass	Neutral density n ($kg.m^{-3}$)	Potential Temperature θ (°C)	Salinity S (psu)
AAIW	Antarctic Intermediate Water	$27.0 < \gamma n < 27.5$		
AASW	Antarctic Surface Water	$27.5 < \gamma n < 28.03$		
CDW	Circumpolar Deep Water	$28.03 < \gamma n < 28.27$	$\theta > 1.5$	$S > 34.5$
MCDW	Modified Circumpolar Deep Water	$28.03 < \gamma n < 28.27$	$\theta < 1.5$	$S < 34.7$
HSMCDW	High Salinity Modified Circumpolar Deep Water	$28.03 < \gamma n < 28.27$	$\theta < 1.5$	$S \geq 34.7$
MSW	Mixed Shelf Water	$\gamma n > 28.27$	$\theta > -1.85$	
AABW	Antarctic Bottom Water	$\gamma n > 28.27$	$\theta > -1.7$	$S > 34.6$
HSSW	High Salinity Shelf Water	$\gamma n > 28.27$	$Tf < \theta < -1.85$	$S < 34.72$
ISW	Ice Shelf Water	$\gamma n > 28.03$	$\theta < Tf$	

timate were computed. These were used to generate a random sample, from a bivariate Normal distribution, from which 200 random pairs of latitude/longitude coordinates were extracted for each position. Bathymetry associated with these 200 samples was then extracted and a mean bathymetry for each position was computed.

To define the shelf area and the continental slope, the inflection point in meridional bathymetric contours, which represents the shelf break, was identified for each half degree of longitude from 0 to 150°E. The boundary between the continental slope and the open ocean was defined as the region where the influence of the Antarctic Slope Front stops. We used pressure gradient on an isopycnal computed from historical Argo floats and ship observations of the region to dynamically define the influence of the slope front and associated it with, roughly, the 3500 m isobaths for our region. Each dive position of seals was attributed either to the shelf, slope or the open ocean area.

Sea ice concentration was extracted from AMSR-E daily sea ice concentration images for years 2004–2011 (http://www.iup.physik. uni-bremen.de:8084/amsr/amsre.html) and derived sea ice maps from SSMI/S were used for the year 2012. Although AMSR-E resolution (6.25 km / 6.25 km) is higher than SSMI/S resolution (13.2 km / 15.5 km), the same algorithm was applied and the grid spacing of 6.25 km was kept. The AMSR2 satellite was used for 2013. Each "grid cell" has an allocated sea ice concentration from 0% to 100%. Finally, we accounted for location uncertainty as described above (step 4 of Figure II.1). Ice concentrations were grouped into three categories based on their frequency distribution: class 1 ([ice] ≤ 5%), class 2 (5% < [ice] ≤ 80%) and class 3 (80% < [ice]).

2.4 Habitat use

We compared the proportion of time spent in several habitats: (a) different areas (i.e. shelf, continental slope, pelagic zone); (b) different water masses; (c) different sea ice concentrations; and (d) different seasons (i.e. summer defined by February, autumn by March–May,

winter by June–August, and spring by September–November). We then tested if the time within each habitat type was significantly different between males and females by applying a Wilcoxon–Mann–Whitney test.

2.5 Statistical analysis of oceanographic conditions in foraging zones

The influence of hydrological features, sea ice concentration and sea floor topography on foraging behaviour (estimated PEE per day) was quantified using GLMMs (step 6 of Figure II.1; Appendix A, section A). Bathymetry, slope and sea ice concentration values were averaged for each seal each day and the most frequent water masses encountered at the bottom phase of dives each day were used. Two models were built, one for each sex, based on 11 females and 17 males including trajectories from 55°S to the Antarctic continent. Explanatory co-variables included factor variables such as class of sea ice concentration, water masses at the bottom phase of dives and continuous variables such as the day of the year, the seabed depth and the slope index associated with topography features. The same process was followed for the 2 models; a negative binomial distribution was used for the error structure of the response variable and individuals were included as random factor.

3 Results

3.1 Trajectory and diving features

A total of 72,209 and 211,909 dives were recorded for the 37 post-breeding (training) and the 35 post-moulting (study) seals respectively, with an average track duration of 29 ± 17 days where accelerometry data were available (mean ± standard deviation) and 159 ± 75 days, respectively. Within each dataset (training and study), diving features are presented in Table II.2 by separating demersal dives from pelagic ones.

Animals from the training dataset made 65.2 ± 12.1 dives per day and travelled 49.8 ± 30.1 km per day (Table AX1), compared to 40.1 ± 17.5 dives per day and 38.7 ± 33.2 km per day for the study animals (Table AX2). Some of the difference between the two datasets might arise from the non-transmission of some dives when the animal is surfacing for the Argos tags (study dataset). Demersal dives represented 5% of dives for the training dataset (only females) and 21% of the study dataset (8% of females' dives and 35% of males' dives).

Thirty one of the 35 study animals travelled to the Antarctic continent, remaining in the seasonal sea ice zone (Figure II.2). Some seals stayed exclusively within the sea ice zone while others had pelagic sorties out of the pack ice. Sex and individual differences were observed and are described in Section 3.3.1.

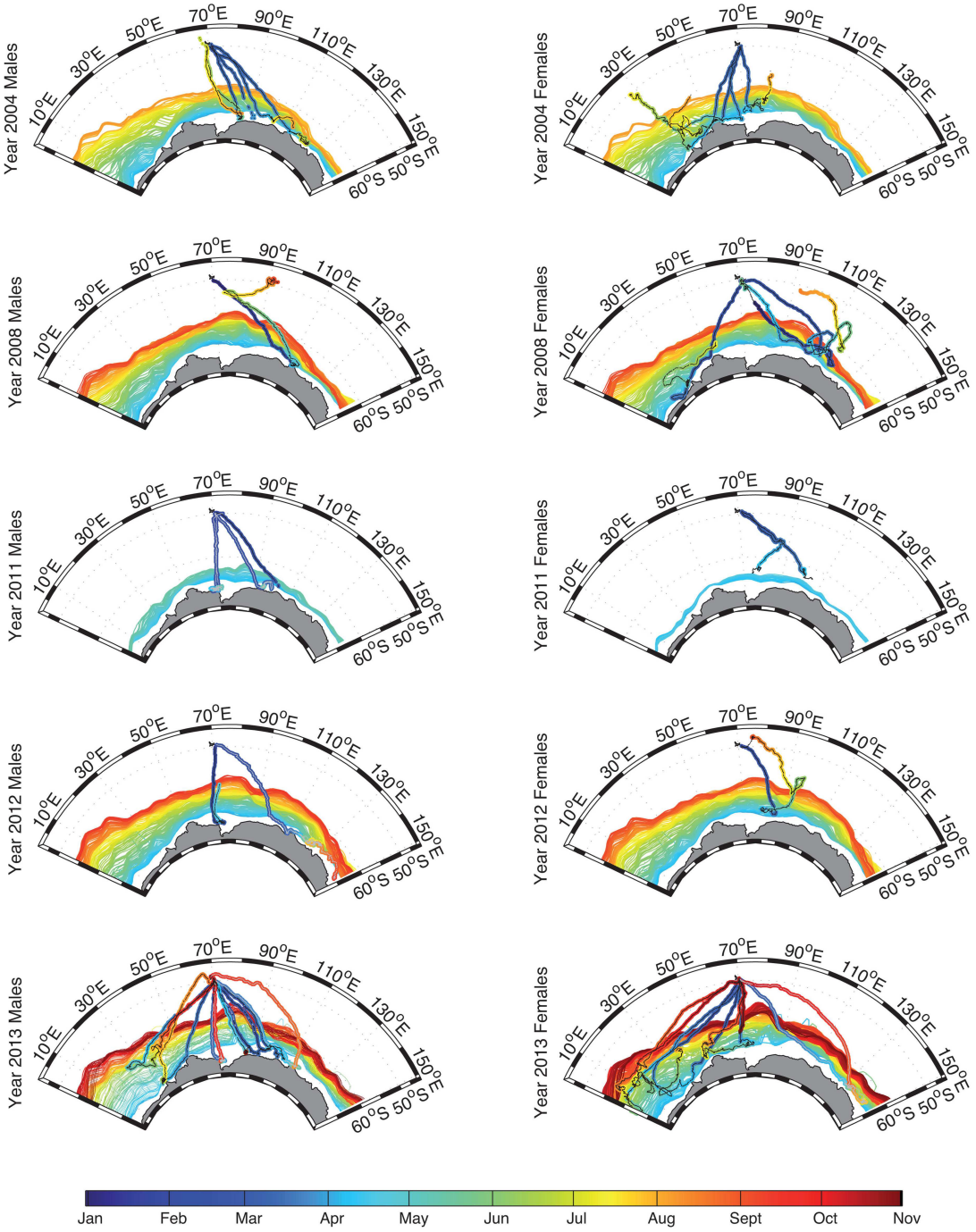


Figure II.2: Tracks per year of the 35 post-moulting SESs equipped with CTD-SRDLs from 2004 to 2013 (study dataset), linked with the seasonality of the sea ice in the East Antarctic region. The colour scale represents the time expressed in month and the same scale is used for sea ice extent and tracks of animals; each sea ice line represents the maximum extent for a given day. Tracks of animal following the sea ice edge as sea ice extends are represented by a black line, while ones remaining in high sea ice concentration independently of the sea ice extension are represented by a grey line. Sea ice extent lines start from April for all years and were computed from AMSRE, SSMI/S product and AMSR-2 satellite data. For each year, tracks of post-moulting animals are represented (left: males, right: females). The unique individual in 2009 was removed for visual purposes.

Table II.2: Summary of the dive and trajectory statistics for the study dataset (post-moulting SES) and for the training dataset (post-breeding SES) for each dive strategy (i.e. demersal or pelagic).

	Demersal			**Pelagic**		
Study dataset (post-moulting)	**Quantile 25%**	**Median**	**Quantile 75%**	**Quantile 25%**	**Median**	**Quantile 75%**
Maximal depth (m)	290	390	503.8	231.3	380	525
Dive duration (min)	16.1	21	27.1	17	23.5	31.3
Bottom time duration (min)	8.3	12.3	17.6	6.9	11.2	17.4
Speed descent ($m.s^{-1}$)	1.4	1.7	2.1	0.73	1.2	1.6
Speed ascent ($m.s^{-1}$)	0.88	1.2	1.4	0.65	0.97	1.2
Horizontal speed ($m.s^{-1}$)	0.18	0.32	0.51	0.32	0.60	0.98
	Demersal			**Pelagic**		
Training dataset (post-breeding)	**Quantile 25%**	**Median**	**Quantile 75%**	**Quantile 25%**	**Median**	**Quantile 75%**
Maximal depth (m)	460.9	545.5	591.4	356.5	491	674.8
Dive duration (min)	16	18.3	20.7	16	18.8	21.7
Bottom time duration (min)	7	9.5	11.9	6.1	8.6	11.1
Speed descent ($m.s^{-1}$)	1.1	1.7	2.3	1.1	1.5	1.8
Speed ascent ($m.s^{-1}$)	1.2	1.5	1.7	1.2	1.4	1.5
Horizontal speed ($m.s^{-1}$)	0.03	0.26	1.1	0.38	0.68	0.95

3.2 Foraging behaviour

3.2.1 Predictive model of foraging activity: diving predictors and performance

The training dataset was used to build the models of foraging behaviour relating observed PEE to dive and trajectory parameters. The demersal model was built with 60 days of observations from 8 different females. The pelagic model was built with 984 days of observations, using all 37 females.

For the demersal model, retained variables after checking colinearity were ascent speed, maximum depth of the dive, dive duration and turning angle, but only ascent speed and dive duration were retained as significant after the stepwise procedure. In the full model, 79% of variance was explained by fixed effects (marginal R2) and 82% by both fixed and random effects (conditional R2) (Table II.3). Regression coefficients computed using leave-one-out cross-validation (CV) (see Appendix A, section A) (Table II.3) indicate low individual variability and increased PEE with increasing ascent speed and dive duration. Ascent speed had the largest predictive value of the model. The predictive ability of the model was assessed using CV, and explained 53% of the deviance.

For the pelagic model, the use were ascent speed, maximum depth of the dive, bottom time duration, horizontal speed and turning angle, of which four were retained after the stepwise procedure (turning angle was removed). Based on this model, 39% of the variance was explained by fixed effects (marginal R^2), and 67% by both fixed and random effects (conditional R^2) (Table II.3). Regression coefficients indicate that PEE increased with increasing bottom phase duration and ascent speed, and decreasing maximum depth and horizontal speed. Maximum depth and ascent speed represented the most important con-

Table II.3: Summary of regression coefficients and goodness-of-fit indices from the two generalized linear mixed effects models of Prey Encounter Events (PEE, based on high-frequency sampled activity data) as a function of various summary dive parameters, based on 37 post-breeding females (training dataset). Separate models were fitted for demersal and pelagic type dives.

	Pelagic Model (n = 984, 36 females)	**Demersal Model (n = 60, 8 females)**
	Quasi-poisson distribution	**Quasi-poisson distribution**
Explanatory variables	**Coef ± SE**	**Coef ± SE**
Intercept	6.20 ± 0.02	5.47 ± 0.11
Maximum depth	-0.28 ± 0.01	/
Dive duration	/	0.44 ± 0.05
Bottom-time	0.09 ± 0.02	/
Speed ascent	0.28 ± 0.01	0.31 ± 0.12
Horizontal speed	-0.21 ± 0.01	/
Goodness-of-fit		
Deviance explained $_{CV}$	30.36%	52.68%
$R^2_{LMM/GLMM(m)-full}$	38.58%	79.21%
$R^2_{LMM/GLMM(c)-full}$	67.45%	81.97%

tributors of the model. About 30% of deviance was explained by the model. Figure II.3A and II.3C show the predictive ability for the demersal model determined by the CV and Figure II.3B and II.3D the predictive ability for the pelagic model. In the pelagic model, three individuals had some predicted values over-estimated relative to their observed values (Figure II.3B), and a deviation is also observed on MSPE (Figure II.3D). Tracks of these three individuals are mostly composed of demersal daily observations that could explain why they differed from the 33 animals left when they are involved in a pelagic strategy. Moreover, for high PEE between 1000 and 1870 PEE (maximum observed in the training dataset), the model tended to under-estimate the values.

3.2.2 Application and prediction of the foraging activity on the study dataset

Within the study dataset, 19% of daily observations represented the demersal strategy (Appendix A, Figure AX3), of which 15% were from females (6 individuals) and 85% were from males (19 individuals). The pelagic strategy represented 81% of the dataset (Appendix A, Figure AX3), with 58% and 42% of female and male observations respectively, made by 15 females and 20 males.

Mean predicted values obtained from the demersal model were 251 ± 106 PEE/day, less than the mean of observed values from the training dataset of 394 ± 165 PEE/day. For the pelagic model, the mean of the predicted values from the study dataset was of 510 ± 231 PEE/day, similar to the mean of observed values from the training dataset of 585 ± 278 PEE/day. For subsequent analyses, predicted values with PEE/day above 1000 and dive

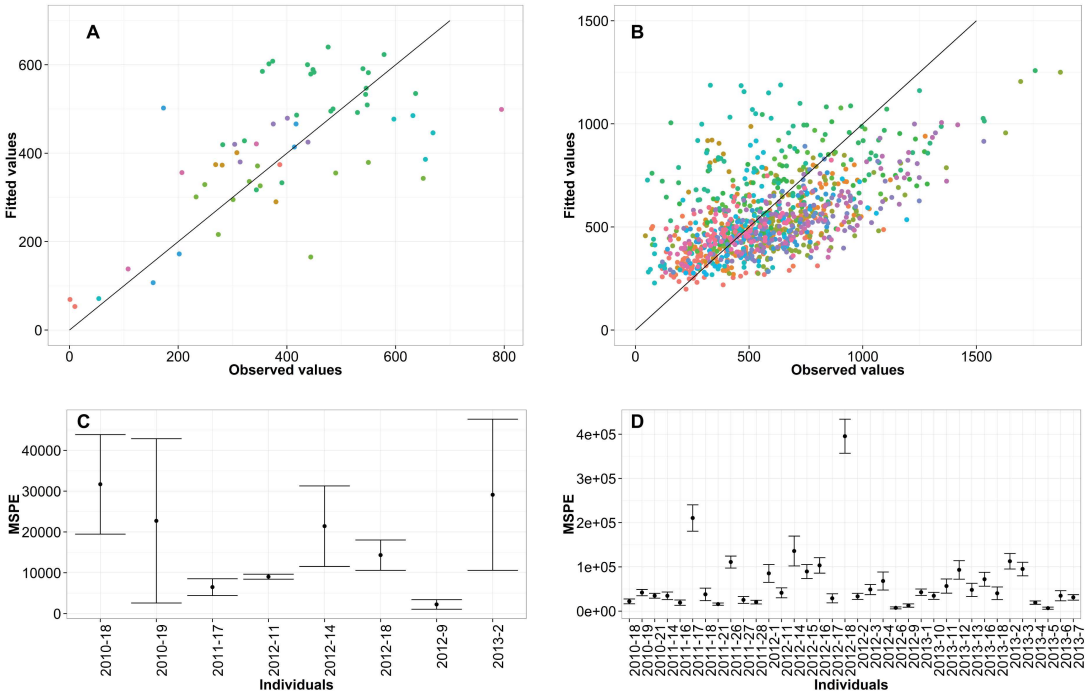


Figure II.3: Predictive ability of behavioural models based on the training dataset of 37 post-breeding females. For A and B, observed versus predicted values obtained after the leave-one-out cross-validation (CV) process are represented for the demersal model (A) and the pelagic model (B). For C and D, MSPE and standard error computed for each individual along the CV process are represented for the demersal model (C) and the pelagic model (D). Colour scale on A and B represents each individual and the line 1:1 is shown, each dot corresponds to one daily observation.

depths ≤ 250 m were removed due to the predictive range of the model. It represented 88 daily observations on a total of 3889 (i.e. 2.3% of the study dataset) from 5 individuals, all of which were males.

Males had on average 418 ± 226 PEE/day and females 494 ± 170 PEE/day. For illustration purposes, we used a threshold of 500 PEE/day, slightly above the average values, to define areas of high foraging activity ("hotspots"). On the shelf, 402 ± 265 PEE/day were observed, 459 ± 180 PEE/day within the continental slope and 481 ± 161 PEE/day for the pelagic area.

Post-moult females had a wide distribution in the East Antarctic region with dominant movements within pelagic areas and the continental slope for some individuals (Figure II.4A). Conversely, male movements were mostly on the south-eastern part of the region within the Antarctic shelf and slope zone (Figure II.4C). Only two males did not exhibit such behaviour; one of which was foraging on the south part of the Gunnerus Ridge along the continental slope and over the shelf (Ind. 2013-4), while the other remained within the pelagic area (Ind. 2013-12).

For females, high foraging activity was mostly localized south of the 4000 m isobaths, within the continental slope/shelf and in pelagic area (Figure II.4A). Conversely, male foraging activity was concentrated principally over the Antarctic shelf and continental slope

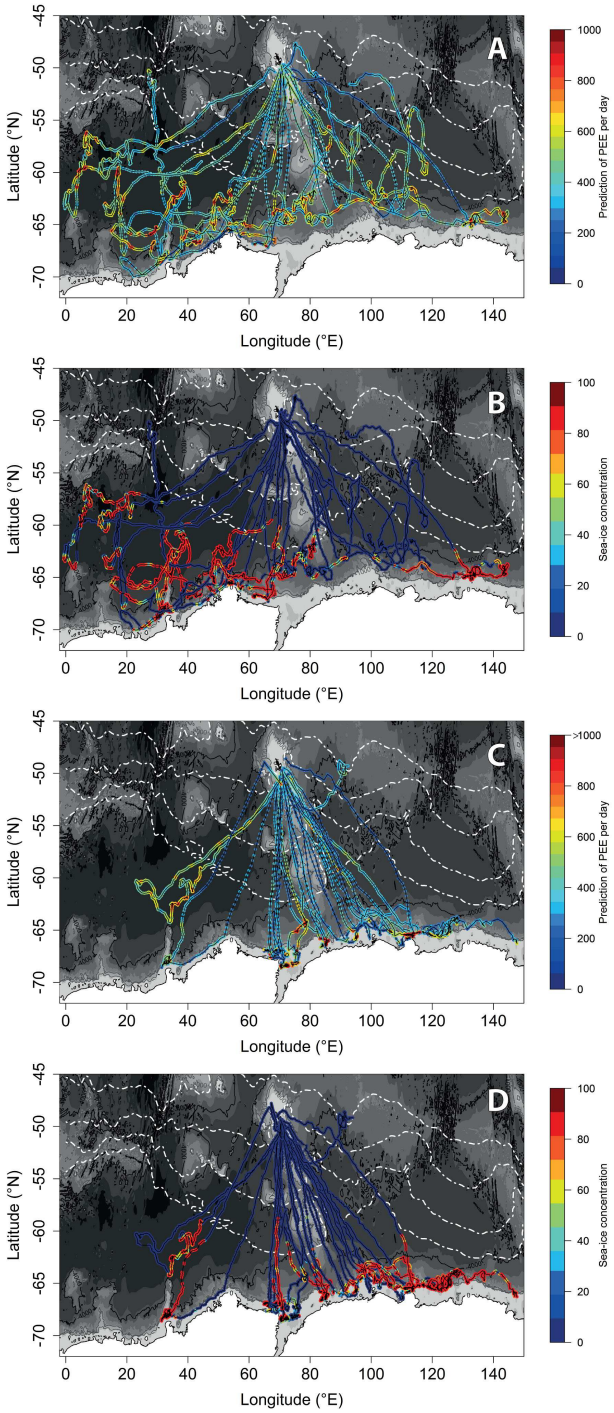


Figure II.4: Tracks of the 35 post-moulting individuals equipped with CTD-SRDLs from 2004 to 2013 (study dataset). For A and C, colour indicates prediction of PEE/day along the track for females (A) and males (C). An interpolation every 12 h was applied for visual purpose. For B and D, colour indicates sea ice concentration associated with females (B) and males (D) filtered positions. A position every 6 h is shown. Oceanic fronts from Roquet et al. [Roquet et al., 2013b] are represented in white dot-dashed lines, from North to South: Sub-antarctic Front (SAF), Polar Front (PF), Southern Antarctic Circumpolar Current Front (SACCF) and Southern Boundary of the Antarctic Circumpolar Current (SB).

with hotspots in the region of Cape Darnley within the Amery Ice shelf and in the region close to 110–115°E within the shelf and shelf break (Figure II.4C). One region around 30°E within the shelf break represented a hotspot used by both males and females (Figure II.4A and II.4C). Foraging areas tended to be located in area of high sea ice concentration along the trip of both males and females (Figure II.4).

3.3 Linking behaviour to oceanographic conditions

From the 35 total individuals, only 28 seals were used; 11 females and 17 males. One individual with short tracks and 6 seals with incomplete hydrological data were removed prior to analysis.

3.3.1 Qualitative approach: description of seals movements within the habitat

Topographic features The twenty-eight seals spent 36.4%, 16.6% and 50% of their time within the shelf, the continental slope and the pelagic area respectively (Figure II.5A).

Over the shelf, the pelagic strategy represented 32% of observations (of which 9% were performed by females and 91% by males) and the demersal strategy 68% (of which 13% were performed by females and 87% by males). Over the continental slope, the pelagic strategy represented 83% of observations (with 48% and 52% for females and males respectively), while the demersal strategy represented 17% (with 18% and 82% for females and males respectively). Deep dives in canyons within the shelf and slope area (previously defined by criteria for demersal strategy; see Appendix A, section A) represented 1.7% of total dives of which 21% female dives and 79% male dives.

Movements within sea ice The seals spent 38% of their time within sea ice concentration of class 1, 28% within class 2 and 34% within class 3 (Figure II.5B).

Sex-specific differences were observed in the movements of animals in relation to the seasonality of the sea ice (Figure II.2). Most females in 2004, 2008, 2012 and 2013 remained in high sea ice concentration inside pack ice, but tended to track the sea ice edge (Figure II.2). In contrast, one female in 2013 travelled to the West along the Antarctic continent despite increased sea ice extent before going back to Kerguelen (Figure II.2). Among males, two different behaviours were exhibited by different individuals throughout the ice covered season: one group of males in 2004, 2012 and 2013 remained within the peri-Antarctic shelf independently of the sea ice extent (Figure II.2); while another group (1 individual each time in 2004, 2008, 2009, 2012, and 4 individuals in 2013) exhibited patterns similar to females (Figure II.2). The latter group arrived on the Antarctic shelf earlier in the season than the other individuals. Figure 6 shows the monthly animals' track versus the monthly sea ice extent variability for the specific year 2013. Females (red tracks on Figure II.6) exploited mostly areas where sea ice concentration was highly variable (except the female travelling to the West) a pattern not observed for males (black tracks on Figure II.6).

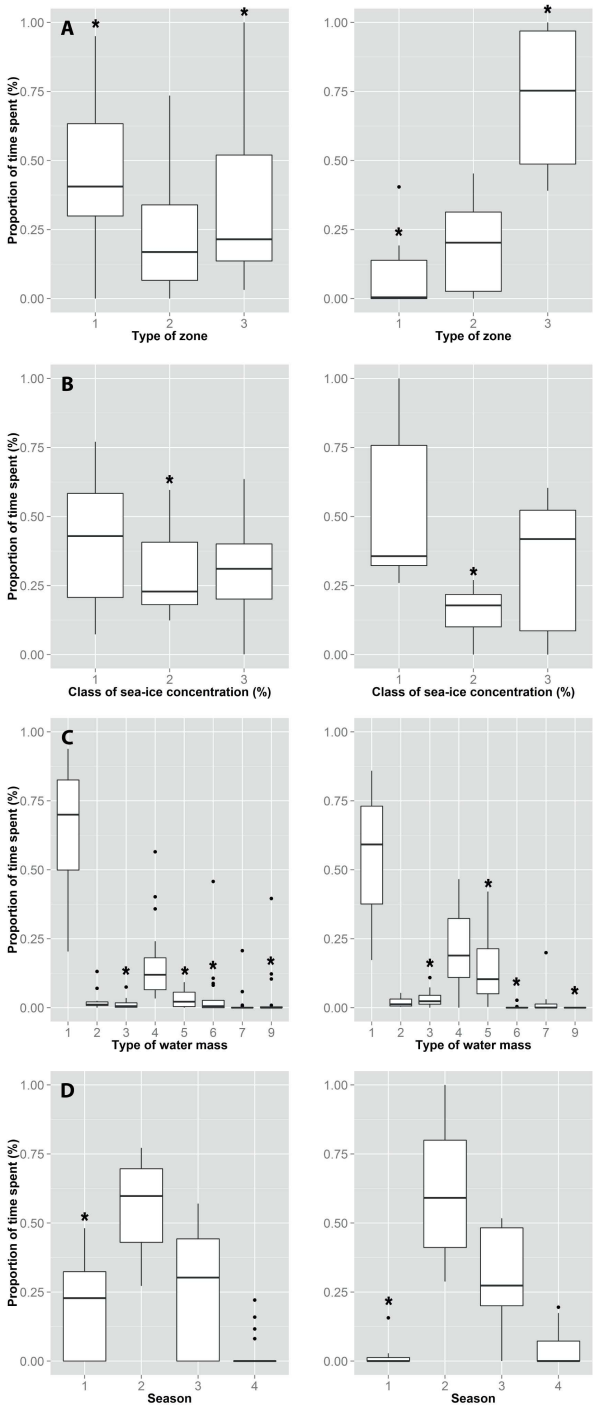


Figure II.5: Boxplots representing the proportion of time spent in each type of environment for the 28 post-moulting animals equipped with CTD-SRDLs from 2004 to 2013 and including tracks from 55°S to the Antarctic continent. Statistics are presented separately for males (left panels) and females (right panels). Part A indicates the time spent in different type of zone, (1) the Antarctic shelf, (2) the continental slope, (3) the pelagic area. Part B indicates the time spent in different type of sea ice concentration, (1) from 0% to 5%, (2) from 5% to 80%, (3) from 80% to 100%. Part C indicates the time spent in different water masses (1) AASW, (2) AAIW, (3) CDW, (4) MCDW, (5) HSMCDW, (6) MSW, (7) AABW, (8) HSSW, (9) ISW. Part D indicates the time spent in different seasons (1) Summer, (2) Autumn, (3) Winter, (4) Spring. Significant differences of time spent in each type of environment between males and females are indicated by a star.

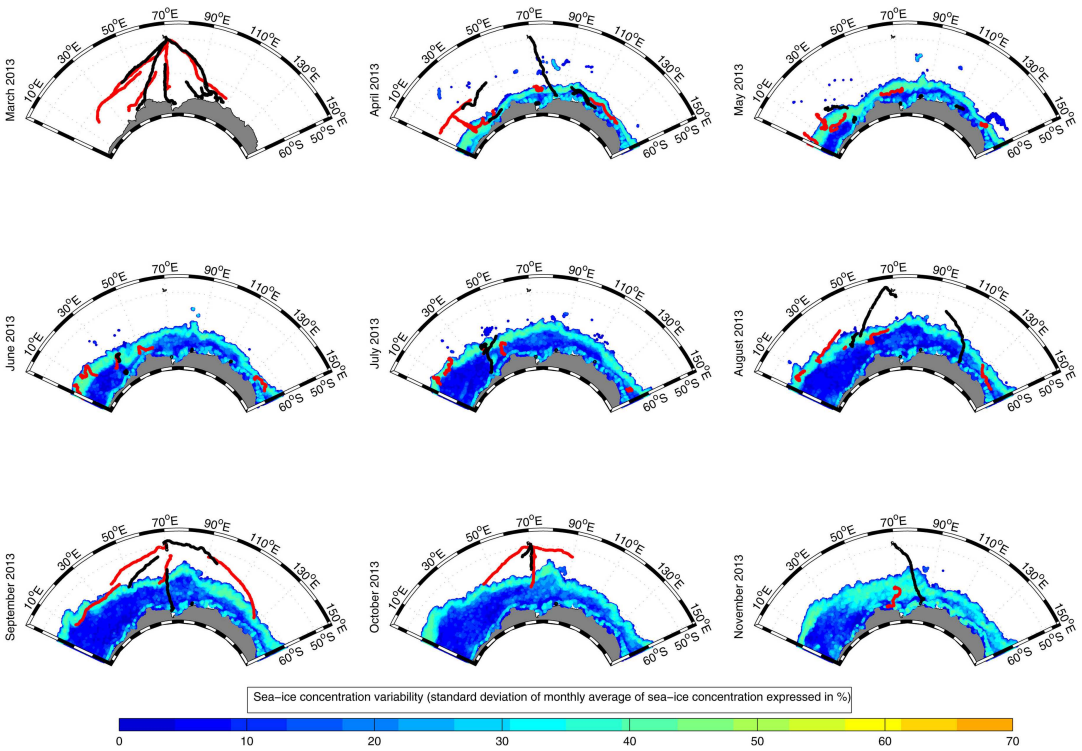


Figure II.6: Tracks per month of the 13 individuals equipped with CTD-SRDLs in 2013 (5 females, 8 males) linked with sea ice variability. The variability is expressed as the standard deviation of the monthly average of sea ice concentration (expressed in %) from AMSR-2 satellite data. Tracks in red correspond to females, while the black ones are for males.

Hydrographic properties A total of 9 water masses were used by the seals during their bottom phase of dives (Figs. II.5C and II.7). Females only rarely visited shelf-associated water masses (i.e. HSSW and ISW). Males and females clearly targeted different water masses for hunting (Figure II.8). While both males and females tended to use hunting hotspots in AASW and MCDW, they used very distinct temperature/salinity classes within these water masses. The largest hotpot for females was in the warmer part of MCDW and AASW, while males favoured mainly the coldest part of AASW. Males also used hotspots of foraging activity in the warmer part of AASW, but to a lesser extent than those in the colder AASW. These distinct TS classes were characteristic of distinct geographic regions. The coldest part of AASW lies over the shelf and over the continental slope [Bindoff et al., 2000], while the warmer AASW is observed further north, in the open ocean, and shallower than the warmer part of MCDW [Bindoff et al., 2000].

3.3.2 Quantitative approach: environmental conditions and foraging behaviour

For males, the most parsimonious model describing PEE/day included all variables except bathymetry (Table II.4): PEE/day was higher for high slope indices, in class 2 of sea ice concentration and in AASW relative to other water masses. However, male PEE/day was

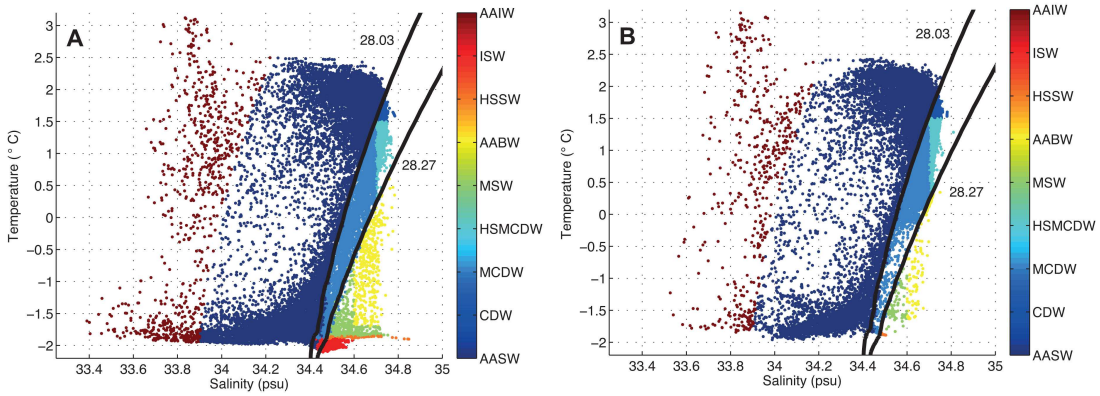


Figure II.7: Temperature salinity diagrams representing all water masses sampled at the bottom phase of dives of the 17 males (A) and 11 females (B) equipped with CTD-SRDLs from 2004 to 2013. Acronyms and definitions of water mass classes can be found in Table II.1.

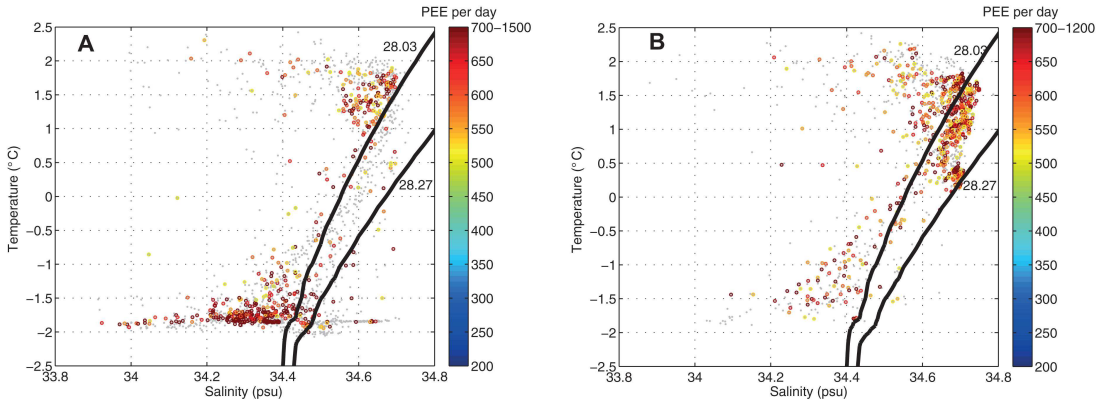


Figure II.8: Temperature salinity diagrams representing hydrologic properties sampled at the bottom phase of dives averaged at the scale of the day of the 17 males (A) and 11 females (B) equipped with CTD-SRDLs from 2004 to 2013. Colour scale represents predicted prey encounter events from behavioural models. PEE per day below 500 is shown in grey as an attempt to highlight foraging hotspots.

significantly lower within the MSW relative to other water masses and with advance of the year. Both AASW and high slope indices correspond to the continental slope area where the Antarctic slope current is observed. High slope indices could be found within canyons as well. For females, the most parsimonious model included all variables (Table II.4). Female foraging activity (predicted PEE/day) was higher for shallower seabed depths, high slope indices, class 3 of sea ice concentration, and within the MCDW. Note that while foraging activity was higher for shallower seabed depths, these shallower depths refer to relatively deep water, north of the continental shelf (females stay mostly north of the continental shelf; see Figure II.4A). Female foraging behaviour (predicted PEE/day) was significantly lower within the AAIW relative to other water masses and with advance of the year.

Table II.4: Summary of regression coefficients from the two most parsimonious models (GLMMs) relating predicted PEE/day to environmental parameters for the 28 post-moulting SESs equipped with CTD-SRDLs from 2004 to 2013. Coefficients are presented ± SE with their p-value associated. Significant parameters are denoted by bold characters. For factor variables (i.e. class of sea ice concentration and type of water mass) coefficients are given relative to the class 1 of sea ice concentrations and AASW for water masses. Signif. codes: 0 "***" 0.001 "**" 0.01 "*".

Negative binomial distribution	**Male Model (n=1774, 17 males)**		**Female Model (n=1419, 11females)**	
Explanatory variables	**Coefficient ± SE**	**p-value**	**Coefficient ± SE**	**p-value**
Intercept	**5.85 ± 0.08**	**< 2.0.10-16*****	**6 ± 0.04**	**< 2.0.10-16*****
Physiographic parameters				
Bathymetry	/	/	**-0.18 ± 0.02**	**< 2.0.10-16*****
Slope	**0.07 ± 0.01**	**1.4.10-8*****	**0.07 ± 0.01**	**3.2.10-12*****
Sea-ice				
Class 2 of sea-ice concentration	**0.19 ± 0.03**	**1.2.10-9*****	0.02 ± 0.03	0.4
Class 3 of sea-ice concentration	**0.11 ± 0.03**	**0.0008*****	**0.14 ± 0.03**	**3.6.10-8*****
Water Masses				
CDW	-0.14 ± 0.22	0.54	0.08 ± 0.05	0.1
MCDW	-0.02 ± 0.03	0.54	**0.05 ± 0.02**	**0.038***
HSCDM	-0.07 ± 0.07	0.29	-0.01 ± 0.03	0.62
MSW	**-0.25 ± 0.05**	**6.4.10-6*****	0.20 ± 0.15	0.16
AABW	-0.03 ± 0.1	0.78	0.03 ± 0.06	0.56
HSSW	-0.13 ± 0.1	0.16	0.18 ± 0.32	0.59
ISW	-0.08 ± 0.06	0.17	/	/
AAIW	-0.14 ± 0.10	0.16	**-0.31 ± 11**	**0.0035****
Time				
Day of the year	**-0.05 ± 0.02**	**0.0025****	**-0.06 ± 0.01**	**6.1.10-6*****

4 Discussion

4.1 From dives to prey: new approach, limits and perspectives

A key objective of this study was to assess if PEE in SES could be predicted from low-resolution dive parameters at the scale of one day. PEE represent a proxy of foraging activity [Viviant et al., 2009, Gallon et al., 2013] and provide indirect information on the distribution and relative abundance of prey [Naito et al., 2013, Guinet et al., 2014]. The objective was not to predict the exact number of PEE/day but to obtain a relative index of foraging activity for a large number of individuals foraging in Antarctic waters.

4.1.1 Predictive ability, population inference and limitations

Our method has a number of limitations with respect to sample size, foraging area, life stage and sex ratio. Despite these factors, patterns of dive behaviour and path trajectory linked to foraging activity were nonetheless identified. Moreover, predictive models provided important information on foraging activity for low-resolution datasets for which no information on foraging activity was otherwise available. Indeed, most studies on low-resolution

datasets of SES used proxies of feeding activity associated with specific vertical movements (e.g. [Bailleul et al., 2007a]), horizontal movements (e.g. [Dragon et al., 2012a]) or both [Dragon et al., 2012b, Bestley et al., 2012, Bestley et al., 2015] without direct evidence with a foraging metric. Studies using body condition (e.g. [Biuw et al., 2007]) as a proxy of feeding success are complicated by the temporal lag between feeding areas and detectable responses in body condition [Thums et al., 2008, Dragon et al., 2012b].

The limited number of individuals in the training dataset for the demersal model (i.e. 8 out of 37 individuals) reduces confidence in predictions at the population level. However, in view of the behavioural differences observed between the demersal and pelagic dives, a specific model for each foraging strategy was probably still better than considering a global model.

No post-moulting animals feeding close to the Antarctic continent have been equipped with accelerometers due to technical (high memory need of accelerometer data) and field logistics (recapture of the animal) limitations. Thus, both pelagic and demersal predictive models were built on individuals using the frontal zones around the Kerguelen Islands, but subsequently applied to individuals in the Antarctic region. However the animals in the training dataset encounter a sufficient range of environmental conditions to capture a range of behaviours so we assumed that any bias associated with differences in foraging areas is limited.

Furthermore, the models were developed on post-breeding animals and then applied to post-moulting animals, which have different energy requirements and prey abundance. Shallower and longer dives were observed for post-moulting seals compared to post-breeding for both strategies (i.e. demersal and pelagic), leading to a potential overestimation of foraging activity when applying regression coefficients from the training dataset on the study dataset (cf. Table II.3).

Males were not represented in the training dataset. Bailleul et al. [Bailleul et al., 2010a] described marked differences in behaviour according to sex and age, most likely due to different mass and previous investigations highlighted a positive correlation between body size and maximum dive durations [Hindell et al., 2000, Irvine et al., 2000, McIntyre et al., 2010b] while the physical size of animals did not govern the depths utilized [McIntyre et al., 2010b]. Differences in body condition between males and females could also be expected with implications on dive behaviour: for example, juvenile males allocate relatively more energy to lean tissue than juvenile females storing greater proportions as fat [Field et al., 2007a]. The training dataset only composed by females did not allow us to test the gender difference in the relation between dive patterns and PEE. However, only two males in our study had a mass above 1000 kg suggesting most of males were sub-adult males with mass similar to females (Table AX2). We then expected the same sign in the relation for males and females with differences in the strength of the relation depending of the sex.

4.1.2 Dive and trajectory parameters: predictors of foraging activity

The study shows that dive behaviour and path trajectory parameters can be used to predict PEE of SES. Only two variables (dive duration and ascent speed) were needed to predict foraging activity adequately for the demersal model, while four variables (ascent speed, horizontal speed, maximum diving depth and bottom phase duration) were required in the pelagic model.

The metrics for dive time differed between pelagic and demersal strategies, with an important positive contribution of dive duration in the demersal model while only bottom duration was retained for the pelagic model and made a poor contribution to the prediction. The number of PEE/day was lower in the demersal strategy compared to pelagic strategy, and on the shelf compared to the continental slope and pelagic area. Small, schooling prey (e.g. Myctophids; [Koz, 1995, Cherel et al., 2008]) were likely to be targeted by seals foraging in pelagic waters, while larger prey items such as Notothenids and Morids [Bradshaw et al., 2003, Banks et al., 2014] are probably more dominant prey items for seals foraging demersaly on the shelf. Foraging theory predicts that animals exploiting clumped or ephemeral prey such as schooling fish need to invest less time in foraging activities than animals feeding on solitary prey [Perry and Pianka, 1997, Thums et al., 2013, Bestley et al., 2015]. In a demersal dive strategy, longer dives would increase the probability of encountering prey [Mori and Boyd, 2004, Austin et al., 2006]. Between the pelagic and demersal strategies, the differences in selection and contribution of dive time variables and number of PEE/day suggest that optimal dive parameters of elephant seals vary significantly depending on habitat, prey size, quality and distribution [Costa, 1991, Thompson and Fedak, 2001]. Regarding the negative relationship between foraging activity and dive depth for the pelagic strategy, we suggested that seals are likely to obtain a prey items sooner in a high-quality patch (i.e. high average rate of resources acquisition) than in a low-quality patch, thus reducing diving depth as reported by Bestley et al. [Bestley et al., 2015].

Finally, we observed that predators reduced their horizontal speed, increasing their search and encounter rate with prey as suggested by Fauchald et al. [Fauchald and Tveraa, 2003], Thums et al. [Thums et al., 2011] and Dragon et al. [Dragon et al., 2012b] when engaged in a pelagic dive strategy and in areas of high prey density (based on high PEE). Vertical transit rate (ascent speed) was an important predictor of foraging activity for both pelagic and demersal model as previously observed for Antarctic fur seals and SES which adopt higher ascent and descent rates in high-quality patches [Thums et al., 2013, Viviant et al., 2014] probably to optimize the energy gained from prey relative to the energy expended during a dive, but also presumably to quickly relocate the favourable prey patch [Gallon et al., 2013].

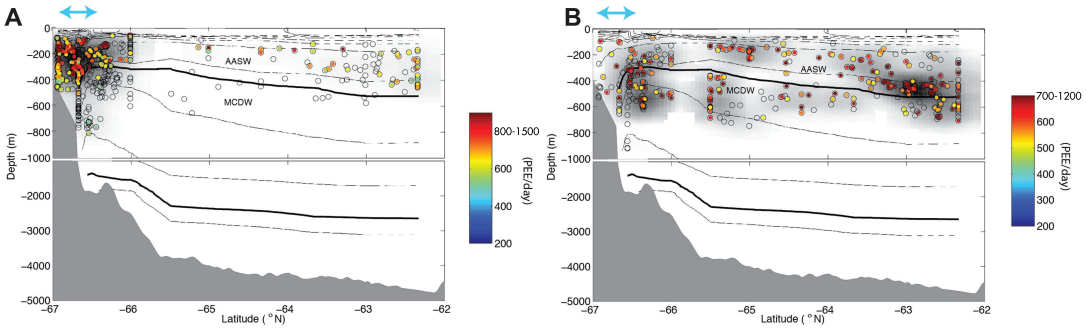


Figure II.9: Projection of the foraging activity in temperature–salinity classes (shown in Figure II.8) onto a high-resolution meridional oceanographic section (along 60°E; [Meijers et al., 2010]). Colour scale represents predicted prey encounter events from the behavioural models for males (A) and females (B). PEE per day below 500 are not colour-coded as an attempt to highlight foraging hotspots. The grey shading in the background corresponds to the sum of PEE per day per grid points: darker areas are associated with a concentration of high foraging events. Bold lines represent the 28.03 kg.m^{-3} (upper) and the 28.27 kg.m^{-3} (lower) neutral surfaces, while dashed lines represent intermediate neutral surfaces every 0.1 kg.m^{-3}. Blue arrows represent the horizontal extent of the Antarctic Slope Front defined by the maximum LADCP zonal velocities observed along the meridional section (from Meijers et al. [Meijers et al., 2010]). Bottom bathymetry along the section is shown in grey.

4.2 Long migration within a remote and constrained environment: linking oceanographic conditions to foraging efforts

We identified the foraging behaviour of elephant seals in relation to oceanographic processes that might influence nutrient availability and resource abundance. We described different strategies adopted by males and females and linked our results with inference about the diet, life-history traits and predictability of foraging grounds.

4.2.1 Female patterns

The distribution of female foraging activity broadly matched the southern extent of the Southern Boundary Front, an important region of high primary production supporting a rich marine ecosystem (e.g. [Tynan, 1998]).

Sea ice played also an important role in terms of the seal distribution patterns. Females mostly exploited coastal regions west of 70°E where short duration of seasonal ice cover is observed in coastal and marginal ice regions west of 85°E [Massom et al., 2013]. Further east (from 70°E to 145°E), females remained over deep waters between 4000 m and 2000 m isobaths again coinciding with the short duration of seasonal ice cover largely confined to the marginal ice zone for the eastern sector [Massom et al., 2013]. Females from Kerguelen may overcome the constraints of sea ice by using areas where sea ice is highly variable or the outer part of the pack ice, enabling them to avoid the risk of getting trapped by sea ice [Bornemann et al., 2000, Bailleul et al., 2007a, Thums et al., 2011, Hindell et al., 2016]. A recent study demonstrated a negative influence of increased sea ice duration on female abundance in breeding colonies at Macquarie Island between 1988 and 2011 with a lag of three years, probably by preventing them from accessing profitable prey patch areas close to the

continental shelf or within the pack ice [van den Hoff et al., 2014]. Observed changes and variability of East Antarctic sea ice season duration from 1979/80 to 2009/10 highlights that in this region sea ice patterns are considerably more complex than the well-documented trends in the western Ross Sea sectors showing extensive increased ice season duration over the past three decades [Massom et al., 2013]. It is then likely that areas of more variable sea ice conditions allow females to benefit from profitable prey patch areas within the pack ice in East Antarctica while minimizing the risk of getting trapped compared to the western Ross Sea.

A key finding of our study was that predicted foraging activity was higher within high sea ice concentration, which is consistent with the seasonal sea ice zone being one of the most dynamic and productive marine ecosystems on Earth [Brierley and Thomas, 2002, Clarke et al., 2008]. During formation, sea ice incorporates particulate matter, so its algal biomass is considerably greater than in the underlying upper water column [Quetin and Ross, 2009] during autumn through early spring (reviewed by Massom and Stammerjohn [Massom and Stammerjohn, 2010]), providing a readily accessible food source for pelagic herbivores such as krill [Meiners et al., 2012]. Extended and high sea ice concentration is usually linked with elevated ice-algal productivity and a higher krill biomass [Loeb et al., 1997, Atkinson et al., 2004]. Krill represents a keystone organism in the Antarctic food chain that could sustain higher predators including SES foraging within the pack ice [Nicol, 2006, Schofield et al., 2010, Walters et al., 2014].

The hydrographic properties of hotspots of foraging activity suggested that female SES feeding south of the 4000 m isobaths within the pack ice and over middle basins dived through the cold AASW to target discontinuities such as the transition between the AASW and the MCDW. The MCDW may represent important overwintering areas for mesopelagic fauna such as zooplankton, fish and squid [Schnack-Schiel, 2001, Lawson et al., 2004, Biuw et al., 2007]. Females were also foraging in areas close to the Antarctic shelf and within the continental slope where intrusion of MCDW brings relatively warm and nutrient rich water onto the continental shelf stimulating primary and secondary production in the region [Prézelin et al., 2000]. These results are clearly illustrated in Figure II.9B, where TS classes of Figure II.8 recorded by females SES were projected on a high resolution meridional oceanographic section (along 60°E; [Meijers et al., 2010]) similar to the study of Biuw et al. [Biuw et al., 2007]. The figure shows an important area of foraging activity along the upper boundary of MCDW and close to the shelf as previously observed by Biuw et al. [Biuw et al., 2007] and Hindell et al. [Hindell et al., 2016]. Interestingly, females also spent an important proportion of time within HSMCDW (the saltiest part of MCDW), which could be used to locate prey patches as it is known that seals may employ high salinity chemo-olfaction for prey location [Sticken and Dehnhardt, 2000]. Foraging activity was significantly lower within AAIW confirming that the area encompassed between the PF and the SACCF is less profitable to SES [Biuw et al., 2007, Guinet et al., 2014].

The ocean properties of areas of high foraging activity can be explained by the presence of potential prey of female SES. For example, the Antarctic silverfish (*Pleuragramma antarcticum*), which is the most abundant pelagic fish in Antarctic shelf water [La Mesa et al., 2010], generally spawns at the sea ice edge [Koubbi et al., 2009] and juveniles are often associated with intrusion of MCDW onto the Antarctic shelf/slope [La Mesa et al., 2010]. Similarly, mesopelagic fish such as the Antarctic lanternfish (*Electrona antarctica*), which usually inhabit deep waters and are found under pack ice feeding on zooplankton [Kaufmann et al., 1995], may also be consumed by SES. A recent study coupling tracking data with fatty acid signature analysis (FASA) on female SES from Macquarie Island, reported that females foraging in the pack ice habitat were likely to have a multi-species diet, i.e. an evenly mixed diet of fish and squid [Banks et al., 2014]. Females may therefore consume various types of prey associated with the sharp discontinuity and intrusion on the shelf of the MCDW and inhabiting the pack ice.

Females foraging in the inter-frontal zone weaned smaller pups than females foraging in Antarctic waters [Authier et al., 2012b]. Thus, Antarctic trips associated with ocean features with predictable enriched resources (such as the MCDW and pack ice habitat), adopted by 25% of females from Kerguelen [Bailleul et al., 2010a], may explain the apparent benefit in terms of pup survival observed in the study of Authier et al. [Authier et al., 2012b].

4.2.2 Male patterns

Our study revealed that sub-adult males mainly travelled and foraged within the south-eastern part of the study area: east of ~ 70°E and in the Antarctic shelf and continental slope regions.

One prominent feature of the male foraging strategy was the number of pelagic dives performed on the Antarctic shelf. Males spent 51% of their time on the shelf where pelagic dives represented 33% of all dives, which resulted in a higher rate of foraging when feeding pelagically. This result contrasts with previous studies assuming that seals within the peri-Antarctic shelf region mostly foraged benthically [Bailleul et al., 2007a, Bailleul et al., 2007b, Biuw et al., 2007, Biuw et al., 2010, Costa et al., 2010, James et al., 2012, McIntyre et al., 2014]. Individuals using a pelagic strategy likely target pelagic fish prey (e.g. *P. antarcticum*) or squid, while those using a demersal strategy likely take deep species such as Antarctic toothfish (*Dissostichus mawsoni*). However, adult toothfish also use the water column and are potentially more common at depths shallower than 200 m than previously thought [Fuiman et al., 2002]. The pelagic dive strategy displayed by males over the shelf/slope region could be a response to a large biomass of prey in the water column, and is an important supplement to the demersal dives (e.g. [Bailleul et al., 2007a, Bailleul et al., 2007b]). The lack of influence of seafloor depth on the foraging behaviour of males and the importance of pelagic dives within the ASF can possibly be attributed to sub-adult males exploiting the seafloor itself less often, compared to adult males (e.g. [McIntyre et al., 2014]). Interestingly, the deep dives within

canyons were mainly performed by males with above average weight (i.e. 664 ± 177 kg; average male weight 553 ± 256 kg), perhaps the only ones physiologically capable of foraging deeper [McIntyre et al., 2010a] and catching bigger prey items such as large squid [Field et al., 2007b] thereby increasing the range of prey sizes and their foraging niche. Another explanation may lie in greater energy requirements of large males forcing them to hunt for larger and/or more energetically rewarding prey in these deep canyons. Further, a few males continuously dived for short periods to depths shallower than 250 m with high PEE (above 1000) on the shelf mostly during winter season when sea ice cover is important. Male SES from King George Island displayed similar behaviour with shallower dives when in high sea ice concentrations [McIntyre et al., 2014]. This new observation could reflect SES foraging on prey close to the surface in response to reduced surface light intensity during winter, such as the Antarctic silverfish (*Pleuragramma antarcticum*) [Fuiman et al., 2002] or even krill associated with sea ice habitat [Walters et al., 2014].

Foraging activity was higher within the continental slope in AASW relative to other regions and water masses. The influence of the AASW is from the coldest class (< -1.6°C; [Bindoff et al., 2000]; Figure II.8A) and TS characteristics show typical waters of the Antarctic Slope Front and shelf waters. High foraging activity was clearly associated with TS classes corresponding on the meridional oceanographic section to a deepening of isopycnals and high horizontal velocity (Figure II.9A). This strongly suggests that the TS classes in which males actively foraged were tightly associated with Antarctic Slope Current jet (ASC) and Antarctic Slope Front (ASF). The ASF corresponds to the strong subsurface horizontal temperature and salinity gradient separating the lighter AASW from the denser MCDW [Meijers et al., 2010]. The significance of the continental slope region to biological productivity in the Antarctic is evident from the potential of upwelling deep water to elevate the early larval stages of krill (*Euphausia superba*) onto the continental shelf [Marr, 1962]. Jacobs [Jacobs, 1991] observed a regionally higher biological productivity along the ASF, which plays an important role in the distribution of sea ice, chlorophyll, krill and cetaceans [Nicol et al., 2000a, Nicol et al., 2000b]. This cold, dynamic and topographically constrained structure, might constitute a deep ocean source region for nutrients [Jacobs, 1991], resulting in higher productivity and enhanced and concentrated resources, which could be detectable in terms of prey availability for SES. Meijers et al. [Meijers et al., 2010] found the ASF extends from the surface to the bottom over the maximum gradient in the shelf break (i.e. depths ~ 500 dbar to 1000 dbar) that could be reached by SES. Two important hotspots of foraging activity were identified for males associated with the ASF. One was situated in the region of Cape Darnley known for the particular "V" shape of the Antarctic Slope Front at 70°E [Meijers et al., 2010]. The second is situated in the region close to 110–115°E within the shelf and shelf break, and matches with observations from [Bindoff et al., 2000] who described a very pronounced horizontal temperature, salinity and density gradient of the ASF at 112°E. Connection between important physical oceanographic features and SES foraging behaviour has been also reported by McIntyre et al. (2012) for males from Marion Island with increased foraging efforts along the South

West Indian Ridge due to higher productivity in mid-water depth layers associated with upwelling [Sokolov and Rintoul, 2007]. Similarly, males from King George Island travelled to the region of the Filchner Trough outflow in the Weddell Sea that supports intensive mixing [Tosh et al., 2009].

The pattern of males remaining on the shelf irrespective of sea ice extent is consistent with results of Bailleul et al. [Bailleul et al., 2007a] and Hindell et al. [Hindell et al., 2016]. However, one group of males did move north with the ice to pelagic foraging grounds similar to the females. This group was mostly composed of smaller seals, probably corresponding to juvenile animals and of two heavier sub-adult animals. Younger and less experienced seals may not take the risk of being trapped by sea ice probably due to mid-year haulouts for these age classes, which agrees with the observed ontogenetic change in foraging ground selection from oceanic to neritic in males [Bailleul et al., 2010a, Chaigne et al., 2012]. As the seals age, they perform longer trips to sea, travelling farther and spending more time closer to Antarctica [Field et al., 2004]. In contrast, the two larger males may have moved north to avoid getting trapped by sea ice, since they are approaching or reached sexual maturity and therefore may prioritize returning to breeding colonies (as suggested by Biuw et al. [Biuw et al., 2010])

Different individuals tended to forage in the same zones (both within and between years) suggesting that the distribution of many prey species associated with some mesoscale features may be predictable to some degree ([Field et al., 2001, Bradshaw et al., 2004, Weimerskirch, 2007]. While opportunistic foraging was observed during transit, most males maintained their trajectory towards the Antarctic continent supporting the hypothesis that elephant seals possess a "memory map" of expected foraging gains in different regions, based on experience from previous years [Thums et al., 2011]. Finally, Authier et al. [Authier et al., 2012a] revealed how a stable foraging strategy developed early in life positively covaried with longevity in male SES. This could explain why similar movements and foraging patterns are observed for males in our study over multiple years.

5 Conclusion

The present study shows that low-resolution dive data can be used to predict the foraging behaviour of apex predators, allowing older datasets to be re-visited.

Over years, females showed a wide distribution with area of high foraging activity mainly south of the 4000 m isobaths, within the pack ice and over mid-depth basins. They targeted the upper boundary of MCDW which may represent important overwintering areas for mesopelagic fauna and avoided being trapped by sea ice by remaining in areas of high sea ice variability. Males predominately travelled to the south-eastern part of the East Antarctica region where they were found to be associated, at a large scale, with the ASF known to play an important role in the concentration of potential prey species of SES. Unexpectedly, hotspots of high foraging activity were associated with pelagic dives within the ASF and not to demersal behaviour on the shelf probably due to their diving capacities

associated with their age. High foraging activity was associated with intermediate sea ice concentration that could be explained by an early arrival in the season on the Antarctic region, restricted trajectories to the Eastern part where sea ice extent is lower or a potential use of coastal polynyas.

Sea ice is an ecological double-edged sword: it can impede access to marine food resources while enhancing biological productivity. However, the precise contribution of sea ice to utilization of the peri-Antarctic region in winter by SES remains unknown.

Further work is needed to identify the type of sea ice used by seals (compact or diffuse sea ice edge, flaw leads, fast ice, polynyas) and how they rely on these features in terms of cost and benefit. Optimal sea ice zones in terms of SES foraging activity probably constitutes an important information source regarding the under sea ice physical and biological habitat, a current “blind spot” that we can investigate using instrumented vertebrates. The complex responses of organisms to sea ice requires to investigate the complete linkage between SES and sea ice and how apex predators and their related resources could be influenced by changes in sea ice in the East Antarctic region.

Acknowledgments

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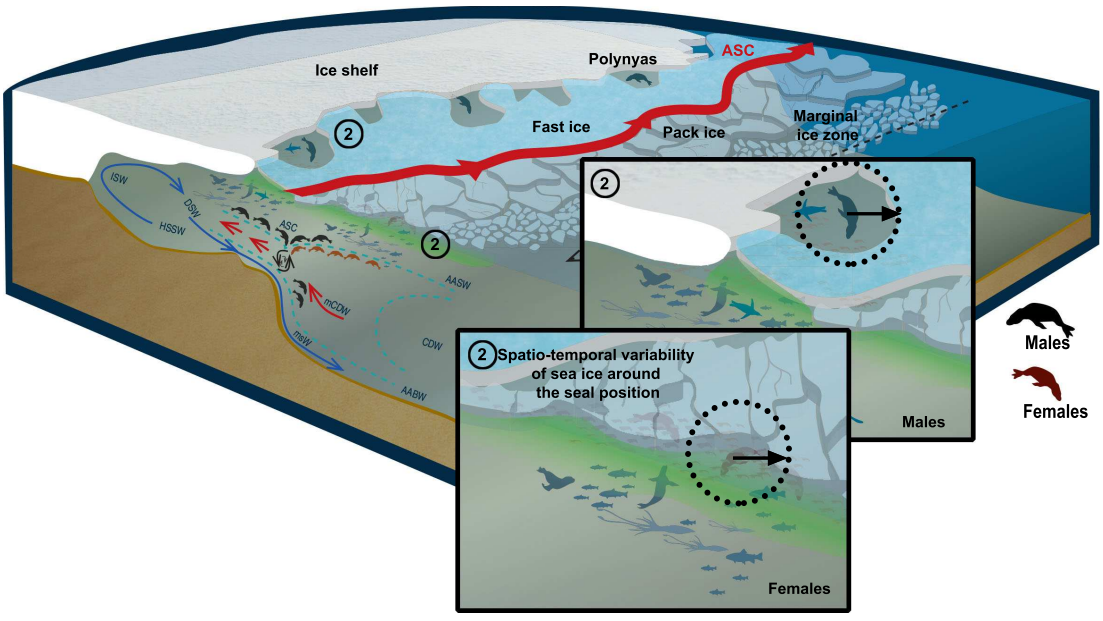
CHAPTER

III

Under the sea ice: exploring the relationship between sea ice and the foraging behaviour of southern elephant seals in East Antarctica

This chapter is under review as *Under the sea ice: exploring the relationship between sea ice and the foraging behaviour of southern elephant seals in East Antarctica* by S. Labrousse, J-B. Sallée, A.D. Fraser, R.A. Massom, P. Reid, M. Sumner, C. Guinet, R. Harcourt, C. McMahon, F. Bailleul, M.A. Hindell and J-B. Charrassin in ***Progress in Oceanography***, 2016.

Schematic of the results from chapter III. Refer to the general discussion 5 for detailed caption.



From the previous chapter, two distinct behaviours towards sea ice were observed between the sexes. Males remained deep within the sea ice despite sea ice extending northward, and had a higher foraging activity within intermediate concentration of sea ice. In contrast, females followed the sea ice edge northward but remained in the pack ice where their foraging activity was higher in highly concentrated sea ice. It was therefore important to further examine their foraging behaviour and movements in response to sea ice conditions. This chapter introduces the concept of constraints and benefits by describing how seal foraging activity is affected by the sea ice cover around its position in space and time and which type of sea ice environment would be constraining and / or beneficial for males and females. This is an important first step in our understanding of the direct and indirect linkages between sea ice conditions and seal foraging behaviour and movements.

Highlights

- Unveil linkages between foraging trips of 46 southern elephant seals and sea ice
- Females follow the seasonal ice edge extent; males remain on the continental shelf
- Females exploit the under-ice ecosystem by foraging below high concentration sea ice
- Males favour the least concentrated sea ice, probably in coastal polynyas and leads
- High variability of sea ice around the seals is key to relax its breathing constraint

Abstract

Investigating ecological relationships between predators and their environment is essential to understand the response of marine ecosystems to climate variability and change. This is particularly true in polar regions, where sea ice (a sensitive climate variable) plays a crucial yet highly dynamic and variable role in how it influences the whole marine ecosystem, from phytoplankton to top predators. For mesopredators such as seals, it both supports a rich (under-ice) food resource, access to which depends on local to regional sea ice coverage and conditions. Here, we investigate gender-specific relationships between the foraging strategies of southern elephant seals (*Mirounga leonina*) in winter and spatio-temporal variability in sea ice concentration (SIC) and coverage in East Antarctica. We satellite-tracked 46 individuals undertaking post-moult trips in winter from Kerguelen Islands to the peri-Antarctic shelf between 2004 and 2014. These data indicate distinct general patterns of sea ice usage: while females tended to follow the sea ice edge as it extended northward, the males remained on the continental shelf despite increasing sea ice. Seal hunting time, a proxy of foraging activity inferred from the diving behaviour, was longer for females in late autumn in the outer part of the pack ice, ~ 150 - 370 km south of the ice edge. Within

persistent regions of compact sea ice, females foraged most intensively (i) in the highest sea ice concentration at their position, but (ii) their foraging activity was longer when there were more patches of low concentration sea ice around their position (either in time or in space; 30 days and 50 km). The high spatio-temporal variability of sea ice around female positions probably allowed them to exploit concentrated patches. Despite lack of information on prey availability, females may exploit the ice algal autumn bloom that sustains krill/copepods and an under-ice ecosystem up to mesopelagic prey without being trapped in sea ice. In contrast, male foraging effort increased when they remained deep within the sea ice (420 - 960 km from the ice edge) over the shelf. They foraged most intensively (i) in the lowest sea ice concentration at their position, and (ii) their foraging activity was longer when there were more patches of low concentration sea ice around their position (either in time or in space; 30 days and 50 km) presumably in polynyas or flaw leads between land fast and pack ice. This provides access to zones of enhanced resources in autumn or in early spring such as polynyas, the Antarctic shelf and slope. Our results suggest that seals utilized a highly sea ice covered environment, which is key for their foraging effort, sustaining or concentrating resources during winter.

1 Introduction

In recent decades, complex regional patterns of change have occurred in both the seasonality and extent of sea ice around Antarctica [Parkinson and Cavalieri, 2012, Stammerjohn et al., 2012], widely affecting the dependent Antarctic marine ecosystem [Massom and Stammerjohn, 2010]. For predators, recent studies have highlighted clear relationships between population dynamics and broad-scale changes and inter-annual variability in sea ice concentration and extent – for both "sea ice obligate" seabird and seal species (e.g. [Barbraud and Weimerskirch, 2001, Barbraud and Weimerskirch, 2006, Proffitt et al., 2007, Siniff et al., 2008, Massom et al., 2009, Forcada et al., 2012, Jenouvrier et al., 2012]) and "non sea ice obligate" species such as chinstrap penguins (*Pygoscelis Antarctica*, [Trivelpiece et al., 2011]) and southern elephant seals (*Mirounga leonina*, [Siniff et al., 2008, van den Hoff et al., 2014]). However, populations have not responded in a uniform way around Antarctica, and contrasting trends are observed that reflect regional differences in climate-induced changes in sea ice properties and in species ecology and biological requirements [Massom and Stammerjohn, 2010, Constable et al., 2014, Southwell et al., 2015]. Many studies exploring the links between sea ice changes and seals focused on the Bellingshausen and Amundsen seas sectors (e.g. [Siniff et al., 2008, Forcada et al., 2012]) or the Ross sea sector (e.g. [Proffitt et al., 2007, Ainley et al., 2015b]) where strongly opposing trends in the extent and the seasonality of the regional sea ice, were observed [Stammerjohn et al., 2008]. However, studies in East Antarctica where patterns of sea ice change and variability are quite complex, comprising mixed signals on regional scales [Massom et al., 2013] are lacking for marine mammals [Weimerskirch et al., 2003]. A major

current challenge involves establishing a better mechanistic understanding of the linkages between climate, sea ice and lower to upper trophic levels in the high-latitude Southern Ocean [Ducklow et al., 2007]. Such information is crucial to allow better prediction of the future response of Antarctic predators to climate change and variability. Finally, while population demographic studies are essential when considering the links between sea ice and marine predators (e.g. in East Antarctica, [Barbraud and Weimerskirch, 2001, Barbraud and Weimerskirch, 2006, Jenouvrier et al., 2012]), they may not in themselves be sufficient to understand the precise nature of the linkages at play; inclusion of information of at-sea foraging behaviour relative to sea ice habitat is also necessary.

For seals, the ice supports a rich (under-ice) food resource because it provides both a substrate for the growth of ice algae and a refuge for herbivorous zooplankton such as juvenile krill and other crustaceans [Marschall, 1988, Flores et al., 2011, Flores et al., 2012b, David et al., 2016], which in turn attracts upper trophic levels such as pelagic fish and their predators [Eicken, 1992, Van Franeker et al., 1997, Reid and Croxall, 2001, Brierley and Thomas, 2002, Tynan et al., 2010, Fraser and Hofmann, 2003]. The access to under-ice food resource depends on local to regional sea ice coverage and conditions [Tynan et al., 2010], thus there is a fine balance between sea ice being either beneficial as it provides access to a rich food source or an impediment for air-breathing marine predators, because of the physical barrier it builds between the ocean and air. The marginal ice zone was also found to be biologically active with concentration of krill, fishes and predators throughout the year [Lancraft et al., 1991, Bost et al., 2004]. However, it is unknown which types of sea ice habitat are most used by deep-diving predators such as southern elephant seals, how they might benefit from the under-ice resources, and how they might overcome the physical constraints associated with the presence of sea ice.

In this study, we combine animal telemetry (i.e. tracks and diving behaviour) and satellite-derived ice concentration data acquired over the different years covering the telemetry study period, with statistical modeling to analyse the interaction with, and reliance on, sea ice characteristics of a "non sea ice obligate" species – the southern elephant seal (SES). Specifically, we investigate the movements (horizontal and vertical) and foraging activity of SESs from the Kerguelen Islands as a function of gender and intra-seasonal variability in East Antarctic sea ice habitat, defined here by sea ice concentration, extent and spatio-temporal variability. While sea ice concentration and extent are critical to Antarctic ecosystems through a possible cascading effect from krill to upper predators [Loeb et al., 1997, Nicol et al., 2000b, Brierley and Thomas, 2002, Fraser and Hofmann, 2003, Atkinson et al., 2004, Flores et al., 2012a], the spatio-temporal variability of sea ice concentration gives important information on the capacity of a sea ice environment to sustain active under-ice ecosystems [Eicken, 1992, Brierley and Thomas, 2002, Nicol, 2006, Clarke et al., 2008, Bluhm et al., 2010, Tynan et al., 2010], and on the sea ice constraint for air breathing predators.

Although considered to be "non sea ice obligate", some SESs interact strongly with the sea ice environment during their long annual migrations from their breeding colonies on sub-Antarctic islands to their high-latitude foraging grounds [Bornemann et al., 2000, Bailleul et al., 2007a, Biuw et al., 2010, Labrousse et al., 2015, Hindell et al., 2016]. Importantly for this study, there are two foraging strategies during the post-moult foraging trips of SESs from Kerguelen Islands; some individuals use the Kerguelen shelf or frontal regions of the Antarctic Circumpolar Current (ACC), while others travel south within sea ice covered areas to reach the peri-Antarctic shelf [Bailleul et al., 2010a]. Moreover, as deep-diving, wide-ranging mesopredators [Hindell et al., 1991b, Hindell et al., 1991a, McConnell et al., 1992] and major consumers of marine resources of the Southern Ocean [Guinet et al., 1996, Hindell et al., 2003b], SESs depend upon an extensive set of trophic levels within the marine food web and their foraging and breeding performances reflect ecosystem status [Trathan et al., 2007]. They also utilize different marine habitats depending on their sex [Bailleul et al., 2010a, Labrousse et al., 2015] and breeding colony location [Biuw et al., 2007, Hindell et al., 2016]. Among the main populations located in the South Atlantic, Southern Indian and South Pacific Oceans, contrasting demographic trends are observed, presumably in response to environmental variability [McMahon et al., 2005, Hindell et al., 2016]. Studying how the environment will modulate the availability of resources for a demographically stable population, such as the Kerguelen Islands population, is essential to use to compare with and help to understand the increasing or decreasing trends observed in the other populations.

This study follows on from previous work on Kerguelen SESs during winter, showing that adult females were closely associated within the marginal sea ice zone, following the northward sea ice extension, and foraging in highly concentrated sea ice close to the sea ice edge [Bailleul et al., 2007a, Labrousse et al., 2015, Hindell et al., 2016]. In contrast, it was shown that juvenile males remained deep within the sea ice foraging mainly over the Antarctic shelf or within the Antarctic Slope Front (ASF) in sea ice of intermediate concentration. The pattern of males diving in waters with low sea ice concentration while on the Antarctic shelf could be explained by either an early arrival in the season in the Antarctic region, movements restricted to sectors where sea ice extent is low, or potentially by use of coastal polynyas [Bailleul et al., 2007a, Labrousse et al., 2015, Hindell et al., 2016]. This study builds upon this previous work by investigating sea ice habitat use using both sea ice concentration and for the first time the spatio-temporal variability of sea ice around the seals' position using a long (i.e. 7 years) and consistent time-series of male and female SESs tracking data. We investigated both the habitat encountered along their tracks and the foraging habitat. However, unlike previous studies we took into account (in each of those linkages) the seals' relative distance from the sea ice edge in an attempt to precisely define the change of sea ice conditions according to the seal movements in the sea ice zone. Finally, we investigated the seasonality of foraging activity when males and females were in the sea ice zone, which has not been previously reported in other studies.

2 Material and methods

2.1 Animal handling, deployment, data collection and filtering

In this study, we use positional and dive pressure data from a total of 46 post-moulting SESs (23 females and 23 males) that were captured and instrumented with CTD-SRDLs (Sea Mammal Research Unit, University of St Andrews) between December and February in 2004, 2008-2009 and 2011-2014 on the Kerguelen Islands (49°20'S, 70°20'E) (details in Appendix B, Table BX1). These animals were chosen from the larger dataset because they visited the area south of 55°S, which is equivalent to the maximum latitude of annual sea ice extent (in September). Unusual behaviour was observed with five animals (two females and three males) returning to the colony before heading back to sea again. For these individuals, the section of tracks where animals travelled again south within the sea ice region (one female and two males) after their return to the colony were removed from analysis. Details of the instrumentation, seal handling and data processing for filtering ARGOS positions are provided by Labrousse et al. [Labrousse et al., 2015]. An average of 18.1 ± 8.6 tag positions were transmitted via the ARGOS system each day. Tags were programmed to record dive depth and time every 4s, from which start time, end time, duration and post-dive surface interval were determined for individual dives. Only the four main inflection points of the time-depth time series, indicating a rapid change of the dive shape, were transmitted for each dive according to tag programming (Sea Mammal Research Unit). For both datasets, a zero offset surface correction was set to 15 m [Guinet et al., 2014]. An average weight of 307 ± 52 kg and 559 ± 244 kg, and an average length of 245 ± 13 cm and 293 ± 39 cm were observed for females and males respectively.

2.2 Sea ice parameters

As in Labrousse et al. [Labrousse et al., 2015], daily estimates of sea ice concentration were derived from satellite Advanced Microwave Scanning Radiometer (AMSR) data at 6.25 km resolution (University of Bremen, http://www.iup.physik.uni-bremen.de:8084/amsr/amsre.html). The data gap for the change from AMSR-E to AMSR-2 in 2012 was filled by data from the Special Sensor Microwave Imager/Sounder (SSMI/S) satellite instrument to provide a consistent and continuous time-series of daily Antarctic sea ice maps from 2004-2014. Although the SSMI/S observations used for 2012 were provided at a lower resolution (12.5 km) than the AMSR observations, the same sea ice concentration algorithm was applied and the grid spacing of 6.25 km was kept for consistency in our analysis.

The distance of seals from the sea ice edge was calculated as the minimum distance between seal positions and the sea ice edge contour, as defined by the 15% sea ice concentration isoline (following Stammerjohn and Smith [Stammerjohn and Smith, 1997]). Contours corresponding to outlying floes or polynyas were removed to prevent bias in our sea ice edge distance computation.

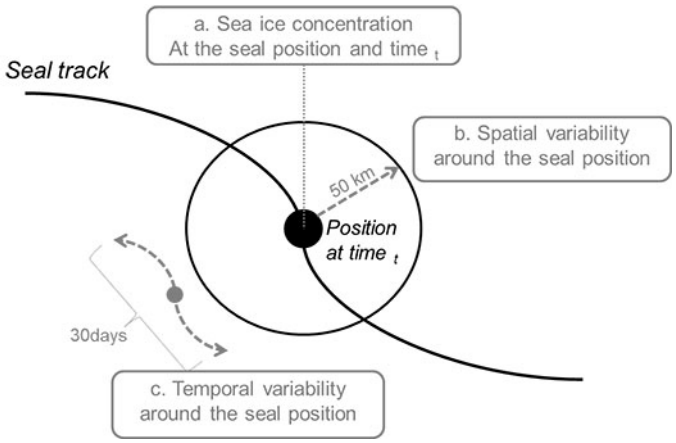


Figure III.1: Schema illustrating the three sea ice variables used in the study: (a) the sea ice concentration at the position of the seal at the present time, (b) the area covered by sea ice with a concentration of > 80% within a 50 km radius around the animal ($A_{80\%}$) and (c) the number of days with a sea ice concentration of > 80%at a given location within a 30 day window ($T_{80\%}$).

Two variables representing the spatio-temporal variability of sea ice around the seal's position were investigated, assuming that sea ice becomes a constraint when the concentration is high. These are: (i) the area covered by sea ice with a concentration of > 80% within a 50 km radius around the animal ($A_{80\%}$; as a measure of the spatial variability of concentrated sea ice patches); and (ii) the number of days with a sea ice concentration of > 80% at a given location within a 30 day window ($T_{80\%}$; as a measure of the time variability of concentrated sea ice patches). A schema illustrating these two variables is shown in Figure III.1.

Finally, the spatial variability of concentrated patches ($A_{80\%}$) showed a strong seasonal signal from March to August-September. Thus, we computed the anomaly of the spatial variability from its seasonal cycle (denoted $A'_{80\%}$; Appendix B, section B). It consisted of (i) computing the median of the observations from the time-series of $A_{80\%}$ for males and females (Appendix B, Figure BX2A – B), (ii) removing this median from each observation to obtain the anomaly of the spatial variability from its seasonal cycle (hereafter denoted $A'_{80\%}$; Appendix B, section B).

2.3 Proxy of foraging activity

Foraging activity of each SES was analysed at the dive scale using the methodology developed by Heerah et al. [Heerah et al., 2015], which estimates the time spent in segments with low vertical velocities (i.e. "hunting time"; vertical speed ≤ 0.4 m.s^{-1}). This time spent at low vertical velocity has been shown to capture most of prey capture events in a separate validation study [Heerah et al., 2015]. In the present study, a long hunting time within a dive does not necessarily mean a high foraging success or high prey availability,

but captures a significant part of the foraging activity occurring during the dive. Heerah et al. [Heerah et al., 2015] found that segments with "hunting time" were associated with four times more prey capture attempts than other segments.

2.4 Statistical modelling of the influence of sea ice parameters on foraging activity

Linear mixed effects models (LMMs) were fitted to examine the statistical relationships between seal foraging activity (expressed by the hunting time per dive) and sea ice concentration, its spatial and temporal variability ($A_{80\%}$ and $T_{80\%}$) taking into account the influence of the season (expressed by the day of year). The different steps of the statistical approach are summarized in Figure III.2. The distance of seals from the sea ice edge within the ice was binned in 6 quantiles for females and males using the R package *Hmisc* (from R Development Core Team, function *cut2*). This variable was then added as an interaction term for all variables. Given the different behaviour of males and females, we constructed a model for each sex. A subset of the data was extracted to only focus on parts of the tracks influenced by sea ice; for this, only positions inside the sea ice and from March (when the seasonal signal of sea ice concentration starts to increase; cf. Appendix B, Figure BX1) to the end of the post-moult trip were used for subsequent analysis. Models were computed with the R package *nlme* (from R Development Core Team, function *lme*; [Pinheiro and DebRoy, 2012]) using restricted maximum likelihood. The hunting time per dive (i.e. response variable) was centred and scaled for each seal prior to analysis to correct for non-Gaussian distribution. Outliers, homogeneity and collinearity in the variables were checked following [Zuur et al., 2010]. Season was highly correlated to $A_{80\%}$ (the later in the season, the higher was $A_{80\%}$), so we did not consider both $A_{80\%}$ and the season in a single model. To disentangle the effect of the season from the effect of $A_{80\%}$, we constructed three different model suites for each sex: (i) including $A_{80\%}$ but without the season (Figure III.2, model 1), (ii) including the season but without $A_{80\%}$ (Figure III.2, model 2) and (iii) including the anomaly of the spatial variability from its seasonal cycle (hereafter denoted $A'_{80\%}$; Appendix B, section B), (Figure III.2, model 3). We present below the model suite (1) including all the sea ice variables, while the two other model suites are presented in Appendix B, Figures BX3 and BX4. Among the different variables (SIC, $A_{80\%}$, and $T_{80\%}$, and the position of seals within sea ice), some collinearities were observed however we did not remove any variables because of likely independent effects on hunting time [Freckleton, 2011]. Explanatory variables were standardized (centered and scaled) to facilitate model convergence and to allow comparisons of the respective contributions of the predictors.

Model selection again followed [Zuur et al., 2010]. We first determined the optimal structure of each model by assessing the full model with fixed effects and their interaction term with and without individual seals as a random intercept term to ensure that this term contributed to the model fit. We then assessed the effect of including an autocorrelation term in the resulting optimal model by using the AR-1 autocorrelation (corAR1) argument.

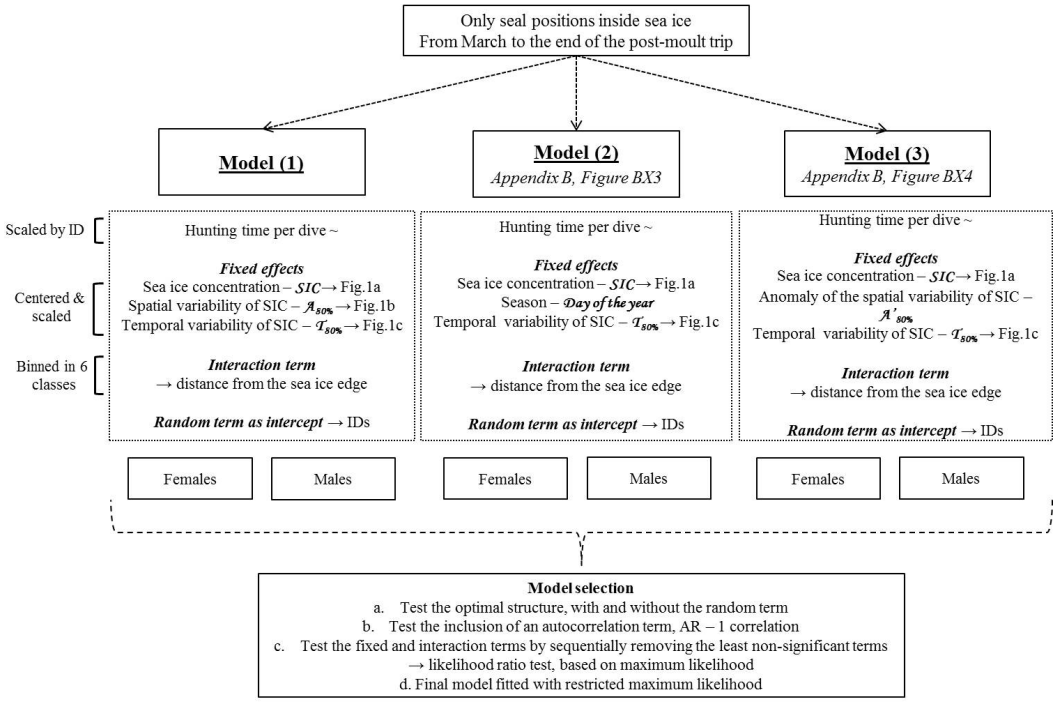


Figure III.2: Schema illustrating the statistical approach step by step used for modelling the influence of sea ice parameters on foraging activity.

Finally, we tested the individual fixed and interaction terms by sequentially removing the least non-significant terms from the model. Model selection was made using the likelihood ratio test, based on maximum likelihood (ML). Terms were only retained if they improved the fit ($p < 0.05$; [Zuur et al., 2009, Bestley et al., 2010]). In all cases, models were ranked via Akaike Information Criterion (AIC) [Burnham and Anderson, 2002], to ensure that the most parsimonious (i.e. lowest AIC value) model was selected. The final model was then fitted using restricted maximum likelihood (REML). All variables were retained in each model. The interaction term corresponding to the distance of the animal from the sea ice edge was also retained in each model, suggesting that the relationship between hunting time and sea ice patterns was influenced by the position of the animal within sea ice at the dive scale.

Model validations were checked by plotting Pearson residuals against fitted values, and against each explanatory variable, verifying homogeneity and normality of residuals [Zuur et al., 2010]. Finally, a marginal R-squared (i.e. variance explained by fixed factors only) and a conditional R-Squared (i.e. variance explained by both fixed and random factors) were calculated as described in Nakagawa and Schielzeth [Nakagawa and Schielzeth, 2010, Nakagawa and Schielzeth, 2013].

3 Results

Data from a total of 286,843 dives were collected for 23 females and 23 males from 2004 to 2014. The combined migration tracks from the Kerguelen Islands in the seasonal sea ice zone are shown in Figure III.3, and statistics and information on each seal are given in Table BX1 (Appendix B). Collation of this information shows a number of gender-specific patterns in relation to their travel to and from, and time and behaviour within, the sea ice zone. Among the 46 individuals from 2004 to 2014, five individuals (four females and one male) did not go into the sea ice: two arrived on the shelf early in the season and left before sea ice formed, two had tag failures or died before they reached sea ice and the last individual did not go enough southwards to reach sea ice. These five seals were removed from subsequent analyses and the study was therefore based on 41 individuals. Males and females left the colony between late December and early March. Females returned to the colony between September and October, and males between September and November (data from animals with active tag transmission, from their departure until return to the colony, 7 females and 8 males). Females travelled 35 ± 28 km per day, and males 32 ± 35 km per day, however when seals were within sea ice, females travelled 24 ± 18 km per day and males 17 ± 18 km per day.

Males, on average, remained further into sea ice (337 ± 267 km from the sea ice edge; maximum 962 km) than females (128 ± 195 km from the sea ice edge; maximum 745 km). Both sexes traveled the furthest within the sea ice zone during the months of May, June and July. The cumulative number of dives of male and female SESs relative to the sea ice extent and their distance from the sea ice edge is shown on Figure III.4. While females tended to follow the sea ice edge as it moved northward (Figure III.4A) males remained mostly on the continental shelf (Figure III.4B). In these environments, the habitat available to seals and male and female preferences in terms of sea ice concentration are shown in Figure III.5. Both males and females used all ranges of sea ice concentration but their habitat differed from the habitat available (Figure III.5), indicating potential preferences and choices made by the animals.

The cumulative dive durations of male and female SESs relative to the 3 sea ice parameters and seal distance from the sea ice edge are shown on Figure III.6. Close to the sea ice edge, both sexes strongly favoured the highest sea ice concentration (90 – 100 % concentration; Figure III.6A, B). This tendency was clearer for females than for males, and even clearer for females moving deeper into the sea ice zone (i.e., 100 – 200 km from the ice edge; Figure III.6B). Males, on the other hand, remained mostly on the continental shelf in regions of less concentrated sea ice i.e., coastal polynyas (Figure III.6A).

On average (±one standard deviation), 37 ± 14 dives per day were collected for females, and 41 ± 19 dives per day for males. These numbers are likely underestimated because of the possibility of non-transmission of some dives when the animal surfaced for too short a duration to allow satellite transmission. For positions only inside the sea ice and from March, the mean time spent hunting per dive was 17 ± 11 min for females and 13 ± 10 min

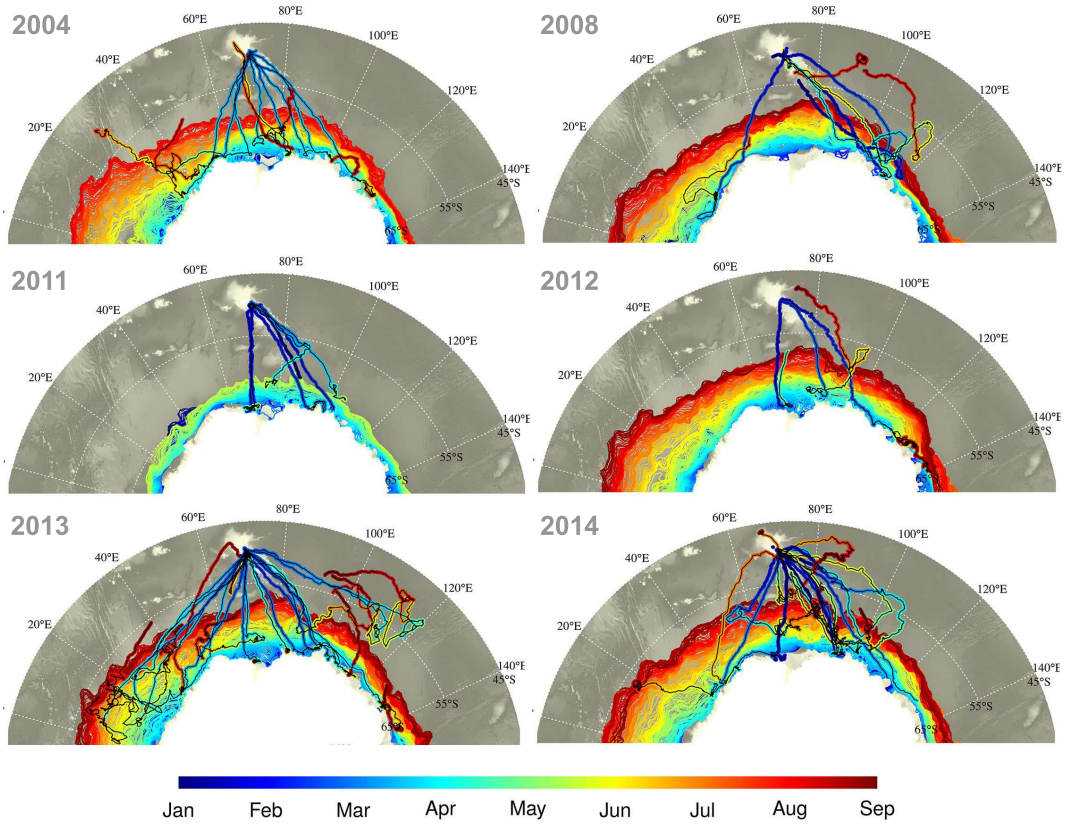


Figure III.3: Tracks of the 46 post-moulting individuals equipped with CTD-SRDLs from 2004 to 2014, linked with the seasonality of the sea ice in the East Antarctic region. The colour scale represents the time and the same colour is used for sea ice extent and tracks of animals; the sea ice extent of a given day and associated seal positions are colored in the same way. For visual purposes, tracks and sea ice extent were limited to September (annual maximum sea ice extent) and the unique individual in 2009 was removed. For all years, sea ice extent was obtained from SSMI/S daily sea ice concentration (resolution 25 km).

for males. The further poleward the seals were from the sea ice edge (per class of distance), the shallower their maximal diving depths i.e., from 446 ± 194 m to 347 ± 212 m for females and from 381 ± 215 m to 247 ± 176 m for males (Appendix B Figure BX5A, B). However, high individual variability does not allow us to conclude about the significance of the relationship between diving depths and the distance from the sea ice edge. Moreover, a southward decrease in dive depth may simply reflect the fact that the bottom topography becomes shallower on the shelf (Appendix B, Figure BX5C, D), so we cannot conclude about the influence of the distance from the sea ice edge on seal diving depth.

Within the sea ice region, 39 individuals (of the 46) performed some shallow dives (i.e. shallower than 40 m) representing 10 ± 6% of the total dives for males and 4 ± 5% for females (Appendix B, Table BX1). For this specific diving behaviour, geographic repartition, frequency of distribution relative to the time of day and their characteristics in terms of sea ice concentration and distance from the sea ice edge are detailed in Figure III.7. Interestingly, 72% of these dives happen during the night (solar angle ≤ -6°) compared to daylight

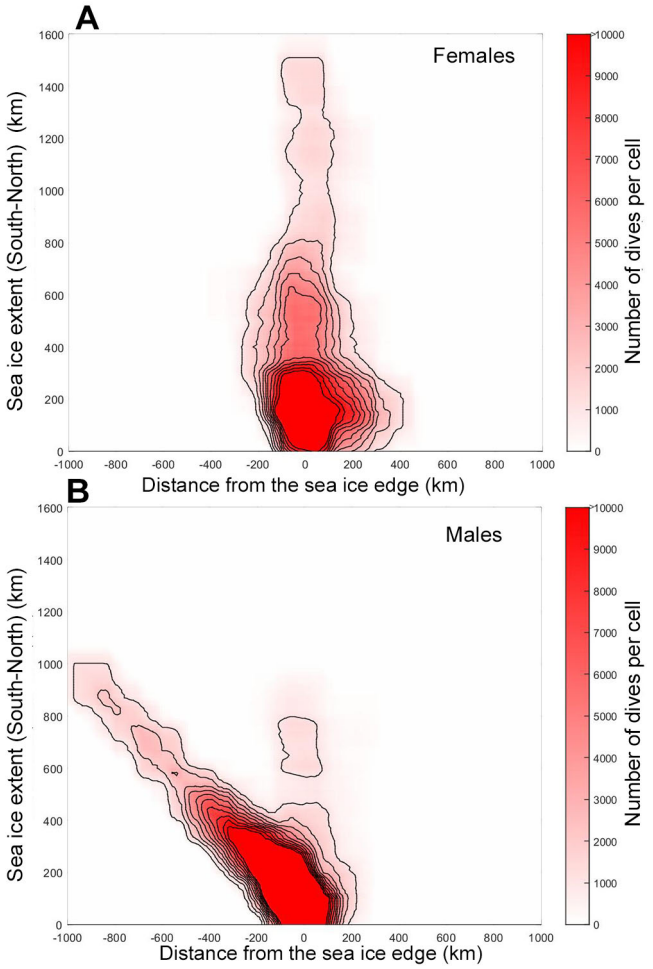


Figure III.4: Density plots of the distance of females (A) and males (B) to the sea ice edge (km) relative to the increase of sea ice extent from South to North (km). Colour intensity represents the number of dives per grid cell of size 10 × 10 km (note that a sliding window over 200 × 200 km has been applied for smoothing purposes). Each contour represents 1000 dives. Negative distances on the x-axis indicate when seals are inside the sea ice region. Animal dives in the open ocean more than 200 km from the edge were not considered as they represent transit from/to the colony.

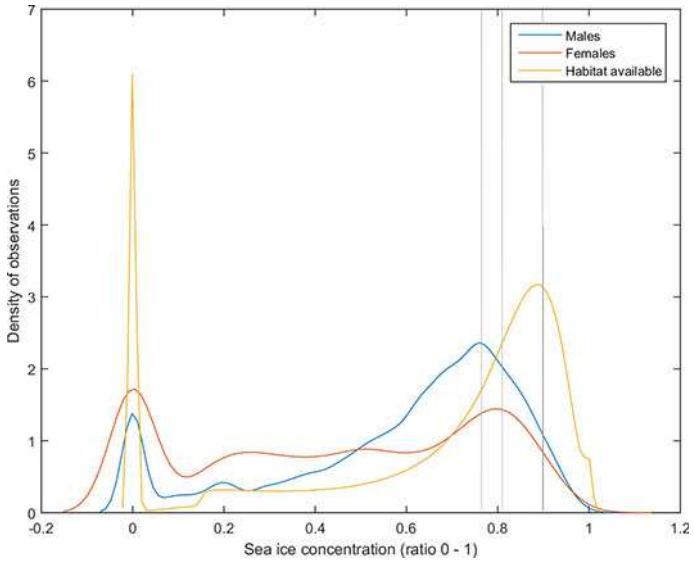


Figure III.5: Density curves representing the habitat available to seals in the area of 0 - 150° E and from 55° S from March to September over the 7 years of the study in terms of sea ice concentration (yellow curve), and the sea ice usage by males (blue curve) and females (red curve). Observations north of 64°S with sea ice concentrations of < 15% were removed. Sea ice concentration was obtained from SSMI/S daily sea ice concentration (resolution 25 km).

(solar angle ≥ 0) and twilight (-6° < solar angle < 0). These dives were often close to the coast, among sea ice concentration of 92 ± 19% and 83 ± 25% for females and males respectively (Figure III.7) and at 133 ± 134 km and 258 ± 219 km from the sea ice edge for females and males respectively. It is the first time such specific behaviour under sea ice has been reported for SESs.

3.1 Influence of sea ice variability on SESs movements

Close to the sea ice edge (from 0 to 100 km), females spent most of their time in transient patches of sea ice ($T_{80\%}$ ~ 10–15 days per month; Figure III.6D) while males dived intensively in patches of both low and high sea ice persistence (low and high values of $T_{80\%}$; Figure III.6C). Females exploited a wide range of $A_{80\%}$, spanning both regions of spatially compact sea ice (up to $A_{80\%}$ of 80%) and very sparsely covered by compact sea ice ($A_{80\%}$ of less than 25%; Figure III.6F). Males mostly remained in regions sparsely covered by compact sea ice ($A_{80\%}$ of less than 25%; Figure III.6E).

Further investigation into the characteristics of high sea ice concentration sectors in which seals foraged reveals distinct differences. For instance, when females ventured further into the pack (100 – 200 km from the ice edge), they encountered persistent and spatially compact sea ice i.e., $T_{80\%}$ ~ 25 – 30 days per month (Figure III.6D) and $A_{80\%}$ ~ 30 – 70% (Figure III.6F). In contrast, areas of concentrated sea ice encountered by males were more transient (i.e. low $T_{80\%}$; Figure III.6C) but still relatively compact spatially ($A_{80\%}$ ~ 30 – 70%; Figure III.6E).

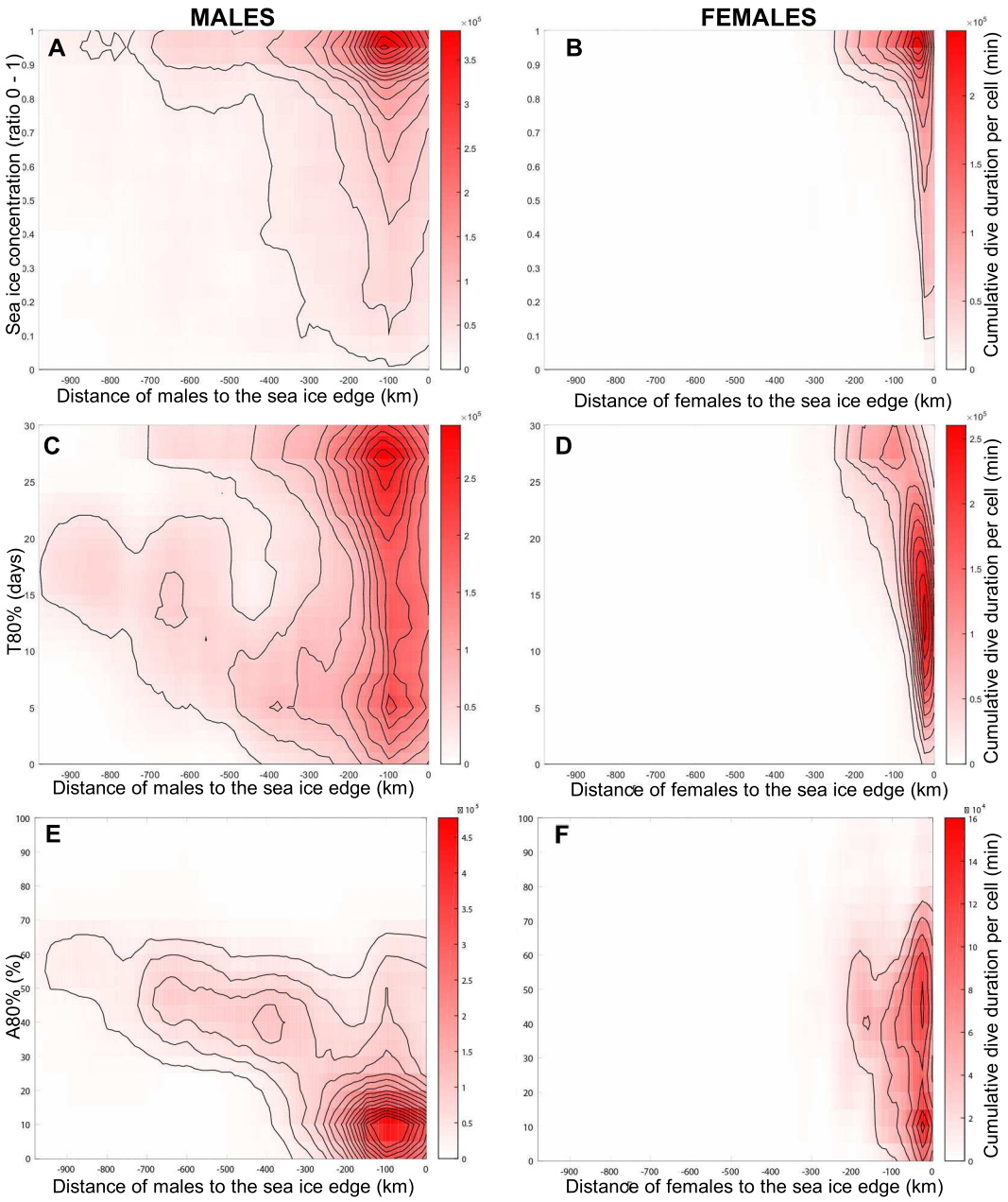


Figure III.6: Density plot of the distance of males and females to the sea ice edge relative to: A, B) Sea ice concentration; C, D) The temporal variability of concentrated sea ice patches ($T_{80\%}$, expressed as the number of days with sea ice concentration above 80% at a given location within a 30 day window); and E, F) The spatial variability of concentrated sea ice patches ($A_{80\%}$, expressed by the area covered by sea ice with concentration above 80% within a 50 km radius around the animal). The colour scale represents the sum of dive duration (in minutes) per grid cell (note that a sliding window has been applied for smoothing purposes). Distances on the x-axis represent when seals are inside the sea ice zone, with values increasing towards the ice edge (at 0 km). One contour is drawn every $0.25.10^5$ min.

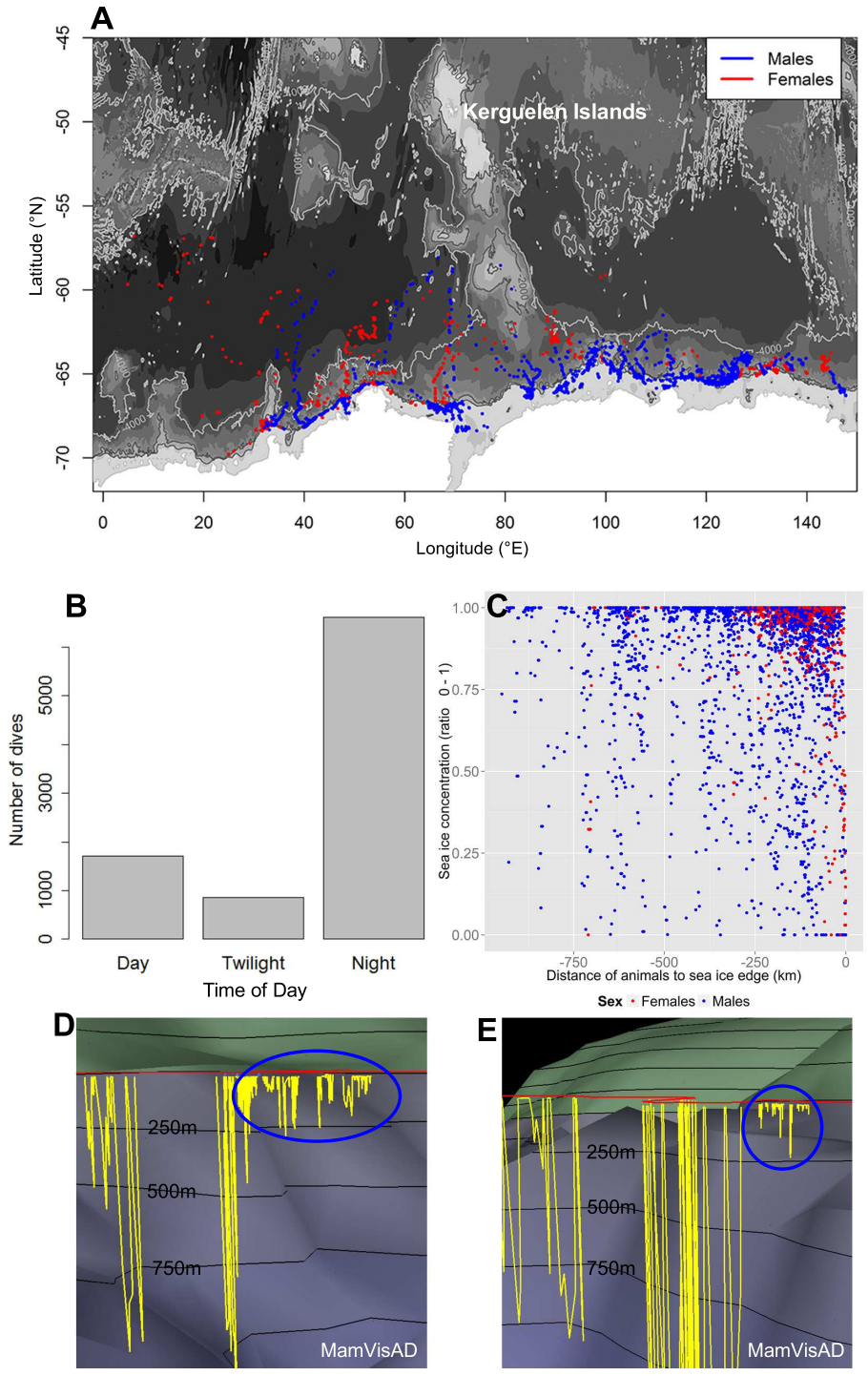


Figure III.7: The characteristics of dives shallower than 40 m for 22 males and 17 females equipped with CTD-SRDLs, from 2004 to 2014. A) Geographic repartition of shallow dives, with blue dots corresponding to male shallow dives and red dots to female shallow dives. The grey shading and contours correspond to bottom topography (m). B) A histogram of the frequency of shallow dives depending the time of day. C) Plot showing the relationship between sea ice concentration (ratio 0 - 1) and the distance of animals to the sea ice edge (in km) for the shallow dives. D-E) Examples of shallow dives for one male and one female, respectively, created with MamVisAD software (from the Sea Mammal Research Unit); dives are represented by yellow lines and red lines being the track of the seal. The blue ellipses show the presence of shallow dives.

Inside the sea ice zone (> 100 km from the sea ice edge), both male and female dives tended to be associated with spatially compact sea ice covered areas (high values of $A_{80\%}$). However, $A_{80\%}$ had a strong seasonal signal, increasing steadily from summer to winter (Appendix B, section B, Figure BX2) and probably associated with the seasonal increase in sea ice concentration (the larger the sea ice concentration, the larger is $A_{80\%}$). This raises the following question: do seals really favour high values of $A_{80\%}$ (i.e. spatially compact sea ice patches) among regions of more or less spatially compact sea ice patches or do our results only reflect seals entering in the pack later in the season, when $A_{80\%}$ is high everywhere? To address this question, one has to consider the sea ice characteristics available to seals. We did this by considering different statistical models, and by seeking to statistically quantify how sea ice characteristics relate to seal hunting time.

3.2 Quantifying the influence of sea ice patterns on SESs foraging activity

A total of 41 individuals (19 females, 22 males) and of 84,964 dives (36,177 for females; 48,787 for males) was used to build the two models. Model results are shown in Table III.1 and Figure III.8; they were divided in different ranges of distance from the sea ice edge. For each variable considered in the model, we present the data that was used to produce the model in each of these ranges (Figure III.8C, D: boxplots for sea ice concentration; Figure III.8G, H: boxplots for $T_{80\%}$; Figure III.8K, L: boxplots for $A_{80\%}$) and the regression lines fitted by the model (Figure III.8A, B: sea ice concentration; Figure III.8E, F: $T_{80\%}$; Figure III.8K, L: $A_{80\%}$). Finally, the influence of the interaction term (i.e. distance of seal from the sea ice edge) on the hunting time is described in Figure III.8M, N.

3.2.1 Summary of model statistics

Both males and females had a longer hunting time when further inside sea ice within their respective regions: males hunted longer closer to the Antarctic continent and females further away from the sea ice edge in the outer part of the pack ice. Habitat use and the relationship between hunting time per dive and sea ice patterns within these sectors are summarized on the diagram Figure III.9. At a given position, females had longer a hunting time in concentrated sea ice while males used low sea ice concentration. Both males and females had a longer hunting time during the autumn season and high spatio-temporal variability of sea ice around their positions (low $T_{80\%}$ and low $A'_{80\%}$) positively influenced their hunting time (Figure III.9).

3.2.2 Model statistics for males and females

Hunting time increased for males deep within the sea ice pack (420 - 960 km from the edge) over the shelf (Figure III.8M) and for females when they were further than 150 km into the pack (Figure III.8N).

Table III.1: Summary of regression coefficients and goodness-of-fit indices from the two most parsimonious models (LMMs) relating hunting time to sea ice patterns for the 19 females and 22 males equipped with CTD-SRDLs from 2004 to 2014. Coefficients are presented ± SE with their associated p-value. Significant parameters at the threshold 5% are denoted by bold characters. Six classes of distance of the animal from the sea ice edge were used in interaction with all the explanatory variables. Coefficients and p-values for the interaction between each explanatory variable and classes 2 – 6 were given relative to the class 1 of distance from the edge corresponding to 0-46 km for males and 0-15 km for females. Individuals were used as random effect on the intercept and explanatory variables were standardized to allow comparison of their slope coefficients. Signif. codes: 0 "***" 0.001 "**" 0.01 "*".

Linear mixed-effects model fit by REML / Response variable: Hunting time (scaled by ID)					
Males (n = 22, dives = 48787)			**Females (n = 19, dives = 36177)**		
Explanatory variables	**Coefficient ± SE**	**p-value**	**Explanatory variables**	**Coefficient ± SE**	**p-value**
Intercept has the baseline value of the class 1 of distance from the sea ice edge					
Intercept	-0.3 ± 0.5	0.5	**Intercept**	-0.5 ± 0.7	0.4
All parameters (for class 1 of distance from the sea ice edge)					
Sea ice concentration	0.1 ± 0.2	0.6	Sea ice concentration	**-0.3 ± 0.1**	**0.03***
Persitence of high SIC ($T_{80\%}$)	**-0.9 ± 0.2**	**0*****	Persitence of high SIC ($T_{80\%}$)	0.6 ± 0.3	0.06
Area covered by high SIC ($A_{80\%}$)	**3.2 ± 0.2**	**0*****	Area covered by high SIC ($A_{80\%}$)	**3.8 ± 0.2**	**0*****
Bin of distance from the sea ice edge (relative to class 1)					
Class 2 [46, 83]	0.008 ± 0.3	0.9	Class 2 [15, 31]	**0.9 ± 0.4**	**0.03***
Class 3 [83,141]	0.2 ± 0.3	0.5	Class 3 [31, 52]	0.2 ± 0.4	0.6
Class 4 [141, 233]	**1.8 ± 0.3**	**0*****	Class 4 [52, 87]	**1.5 ± 0.4**	**0*****
Class 5 [233,417]	**2.1 ± 0.3**	**0*****	Class 5 [87, 147]	**2.7 ± 0.5**	**0*****
Class 6 [417,962]	**4.3 ± 0.5**	**0*****	Class 6 [147, 367]	**3.9 ± 0.6**	**0*****
Sea ice concentration (relative to class 1 of distance from the sea ice edge)					
SIC:Class 2 [46, 83]	-0.08± 0.3	0.8	SIC:Class 2 [15, 31]	-0.5 ± 0.2	0.06
SIC:Class 3 [83,141]	-0.3 ± 0.3	0.3	SIC:Class 3 [31, 52]	**0.6 ± 0.3**	**0.04***
SIC:Class 4 [141, 233]	**-0.9 ± 0.3**	**0.002****	SIC:Class 4 [52, 87]	0.1 ± 0.3	0.7
SIC:Class 5 [233,417]	**-0.9 ± 0.3**	**0*****	SIC:Class 5 [87, 147]	0.6 ± 0.5	0.2
SIC:Class 6 [417,962]	**-1.3 ± 0.3**	**0*****	SIC:Class 6 [147, 367]	**1.2 ± 0.5**	**0.02****
Persitence of high SIC, $T_{80\%}$ (relative to class 1 of distance from the sea ice edge)					
$T_{80\%}$:Class 2 [46, 83]	0.5 ± 0.3	0.08	$T_{80\%}$:Class 2 [15, 31]	0.2 ± 0.4	0.6
$T_{80\%}$:Class 3 [83,141]	0.6 ± 0.3	0.053	$T_{80\%}$:Class 3 [31, 52]	**-1 ± 0.4**	**0.01***
$T_{80\%}$:Class 4 [141, 233]	0.5 ± 0.3	0.09	$T_{80\%}$:Class 4 [52, 87]	**-1 ± 0.4**	**0.02***
$T_{80\%}$:Class 5 [233,417]	0.002 ± 0.3	0.9	$T_{80\%}$:Class 5 [87, 147]	**-1 ± 0.5**	**0.03***
$T_{80\%}$:Class 6 [417,962]	0.1 ± 0.3	0.6	$T_{80\%}$:Class 6 [147, 367]	-1.1 ± 0.6	0.07
Area covered by high SIC, $A_{80\%}$ (relative to class 1 of distance from the sea ice edge)					
$A_{80\%}$:Class 2 [46, 83]	0.3 ± 0.3	0.3	$A_{80\%}$:Class 2 [15, 31]	-0.05 ± 0.2	0.8
$A_{80\%}$:Class 3 [83,141]	**-1 ± 0.3**	**0*****	$A_{80\%}$:Class 3 [31, 52]	0.01 ± 0.3	0.9
$A_{80\%}$:Class 4 [141, 233]	**-1.3 ± 0.3**	**0****	$A_{80\%}$:Class 4 [52, 87]	-0.3 ± 0.3	0.3
$A_{80\%}$:Class 5 [233,417]	**-1.2 ± 0.3**	**0*****	$A_{80\%}$:Class 5 [87, 147]	**-2.2 ± 0.3**	**0*****
$A_{80\%}$:Class 6 [417,962]	**-2.9 ± 0.4**	**0*****	$A_{80\%}$:Class 6 [147, 367]	**-3.2 ± 0.3**	**0*****
Goodness-of-fit					
$R^2_{LMM(m)-full}$	**14%**		***R2LMM(m)-full***	**13%**	
$R^2_{LMM(c)-full}$	**21%**		***R2 LMM(c)-full***	**18%**	

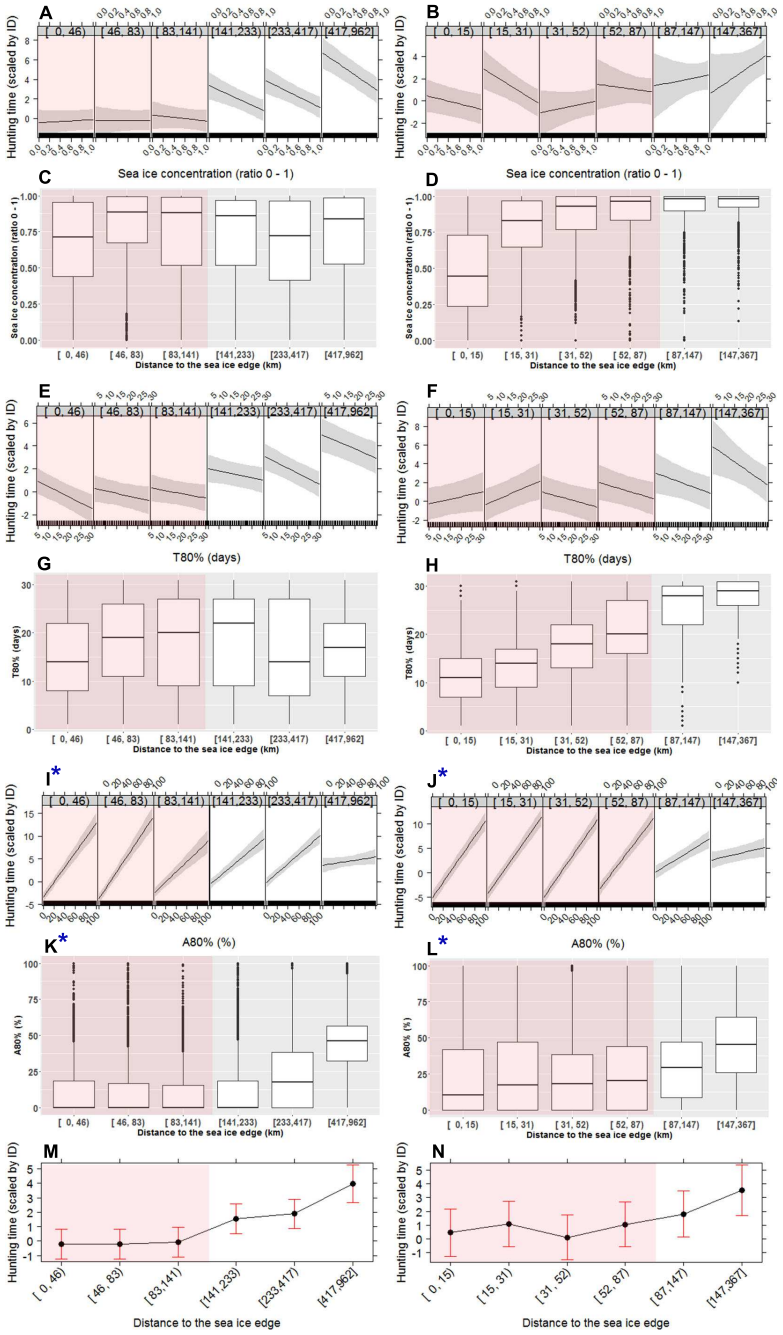


Figure III.8: Model 1, relationships from the two LMMs between hunting time and: A, B) the sea ice concentration at the seal position; E, F) the temporal variability of concentrated sea ice patches ($T_{80\%}$); I, J) the spatial variability of concentrated sea ice patches ($A_{80\%}$); and M, N) the distance of animals from the sea ice edge. Results for males are presented on the left panels and those for females on the right. Each graph from models shows the relationship relative to bin of the distance of the animal from the sea ice edge when inside the sea ice region (in km). For each graph, the thick lines represent the predictive values from the population at a given position in sea ice and the grey shaded envelopes represent the boundaries of the variation between the predicted values per individual. Available data for each bin of distance are represented by boxplots for: C, D) sea ice concentration; G, H) the temporal variability of concentrated sea ice patches ($T_{80\%}$); and K, L) the spatial variability of concentrated sea ice patches ($A_{80\%}$). The marginal ice zone is shown by the red shaded area. The variable differing between the three model suites was represented by blue stars (see Appendix B, Figure BX3 and BX4).

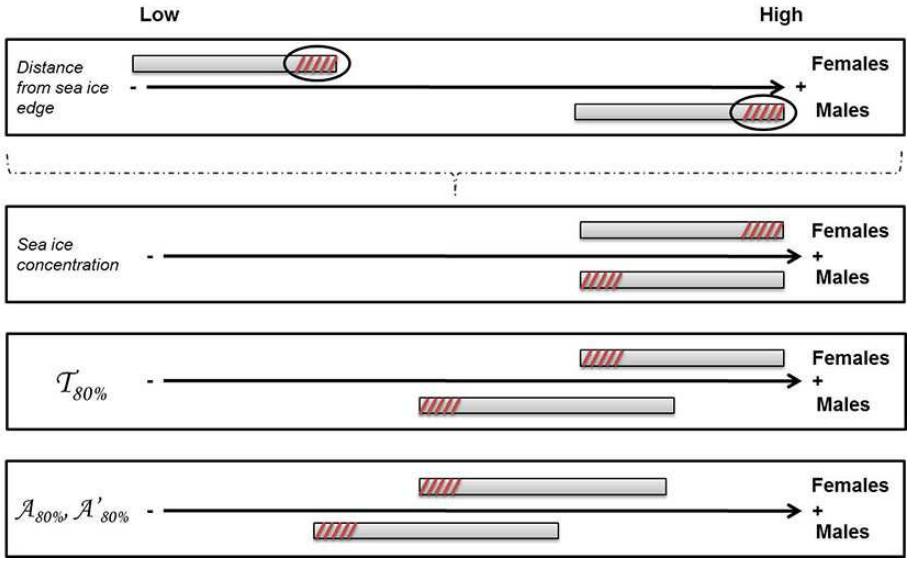


Figure III.9: Summary schematic of the model analysis. Results for sea ice concentration, the temporal variability of concentrated sea ice patches ($T_{80\%}$) and the spatial variability of concentrated sea ice patches ($A_{80\%}$) are presented for sectors where males and females foraged more intensively, i.e. 150 - 370 km from the edge for females and 420 – 960 km from the edge for males. Grey bars represent their habitat use in these sectors, while red hatched lines represent where they foraged more intensively.

Sea ice concentration had a negative influence on male hunting time and this negative influence was greater when males were deeper in the sea ice zone (Figure III.8A). In contrast, female hunting time was positively correlated with sea ice concentration further than 30 km from the sea ice edge. In these regions, females were in high sea ice concentrations (Figure III.8D) where they favored the highest sea ice concentration available for hunting (Figure III.8B).

Males favoured the low values of $T_{80\%}$ for hunting (Figure III.8E), even though they had access to a wide range of different regimes of low to high values of $T_{80\%}$ (Figure III.8G). In contrast, females had access to only relatively high values of $T_{80\%}$ further than 30 km from the edge (Figure III.8H), but like male behaviour, females favored the low values of $T_{80\%}$ (Figure III.8F).

Interestingly, male and female hunting time was always longer for high values of $A_{80\%}$ (Figure III.8I, J). However, as noted above $A_{80\%}$ is correlated with the season, so it is unclear if this result is an indication of seals favouring high values of $A_{80\%}$, or if it reflects seals hunting longer later in the season for other reasons. Given their correlation (r $\sim$ 0.8), it is impossible to clearly disentangle the influence of the two parameters. However, we repeated the same statistical models while removing the seasonal cycle to $A_{80\%}$. For a given time of year, hunting was shorter when $A'_{80\%}$ increased (Appendix B, Figure BX4I, J, K, L). One interpretation would be that hunting time is longer later in the season, but for a given season, it is even longer if seals find patches of sea ice more sparsely distributed (low $A_{80\%}$).

Consistent with this, the statistical model considering season without $A_{80\%}$, indicated that hunting time increased with the day of year (Appendix B, Figure BX3I, J). However, for males this relationship between hunting time and day of year became close to zero when males were further into the pack, i.e. later in the season from about July onward (Appendix B, Figure BX3I and K). Therefore, these results suggested that hunting time increased for males and females with the day of year from about April (day of year 90) to June (day of year 180). For males we found that the relationship with hunting time was lower with day of year from July (day of year 180) to October (day of year 270), suggesting seasonal variability with enhanced foraging conditions in austral autumn/early winter. For females, the lack of observations after July precludes evidence of a reversal after autumn.

Models that included season (Appendix B, Figure BX3) or $A_{80\%}$ (Figure III.9) explained 30% and ~ 20% of the variance respectively (conditional R^2). However, when seasonal cycle of $A_{80\%}$ was removed, the explained variance of the models dropped to 6 - 14% (conditional R^2 for females and males respectively; Appendix B, Figure BX4). This points to the importance of seasonal variability; either the season itself or seasonally variable quantities, such as $A_{80\%}$.

4 Discussion

In the present study, we chose to elaborate on the potential attractiveness of under-ice ecosystems for SESs in terms of resources to explain the strategy adopted by some individuals to forage within sea ice covered areas as opposed to those foraging in the vicinity of the Kerguelen Plateau in frontal zones. However, it is important to note that travelling south within sea ice covered areas may also be an avoidance response of predation by sub-Antarctic killer whales inhabiting the vicinity of the Kerguelen Plateau [Pitman, 2011]. Further research is needed to measure the killer whale predation on SESs foraging in open waters versus in the sea-ice zone, for example using life-history transmitters [Horning and Mellish, 2009], in order to quantify the survival advantage that sea ice as an anti-predation refuge may confer to SESs.

Sea ice characteristics influence foraging behaviour of male and female Kerguelen elephant seals, in markedly distinct ways; here we confirmed the results observed in Bailleul et al. [Bailleul et al., 2007a], Hindell et al. [Hindell et al., 2016] and Labrousse et al. [Labrousse et al., 2015]. We also brought new insights by defining male and female habitat based on their distance from the sea ice edge and by quantifying the relation between foraging activity and sea ice concentration given their distance from the sea ice edge. While females tended to remain within 200 km of the sea ice edge and foraged most intensively in high concentrations of sea ice (see example of tracks in Figure III.10), males tended to remain on the continental shelf, foraging in low sea ice concentrations (see example of tracks in Figure III.11).

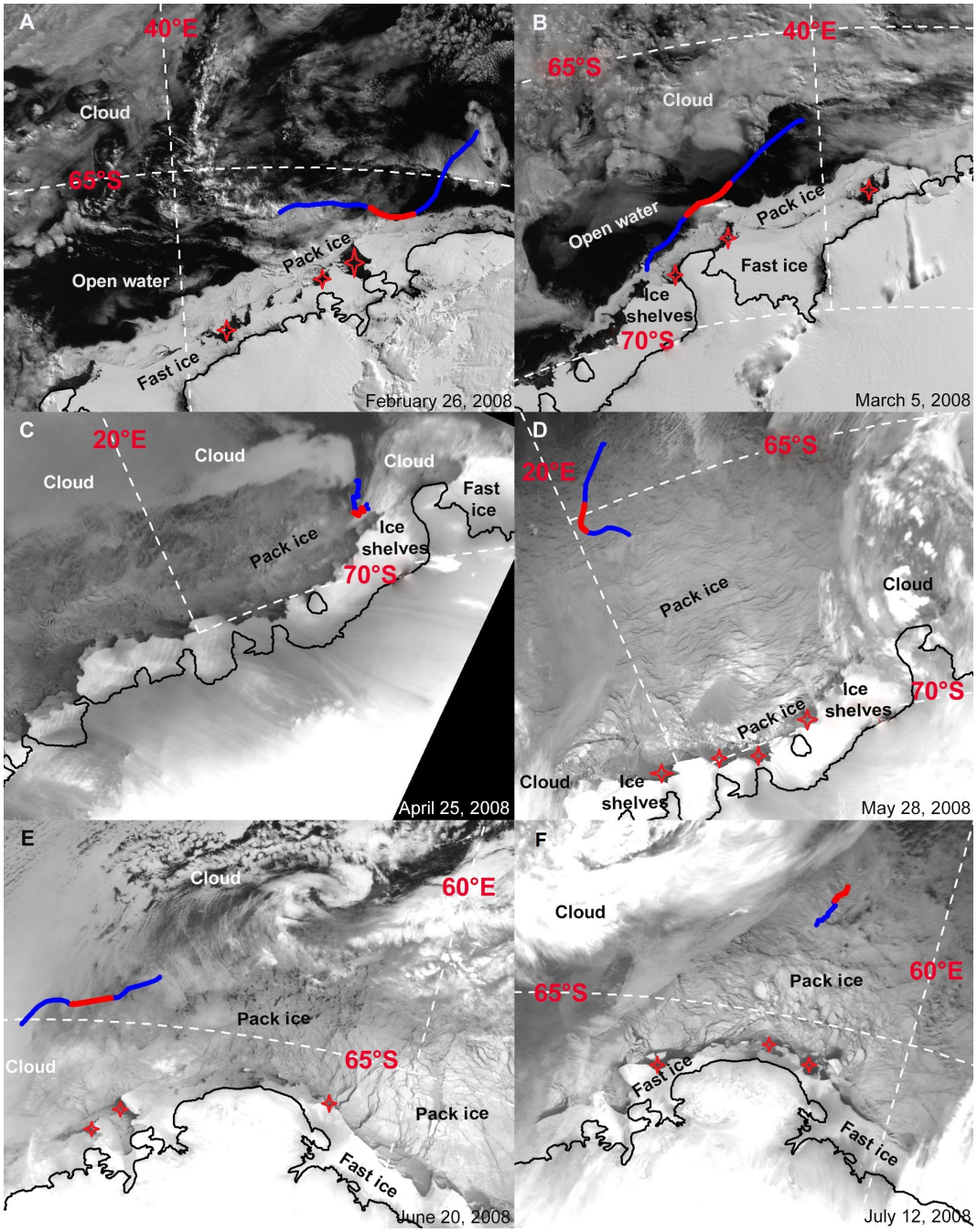


Figure III.10: Time-series of MODIS visible and infrared images of resolution 1 km illustrating female behaviour within sea ice from February to July 2008 within the region from 20 to 50°E. Coincident day animal track is represented by a red curve, while the blue part corresponds to the previous and subsequent two days. Polynyas and large open water areas are represented by red stars.

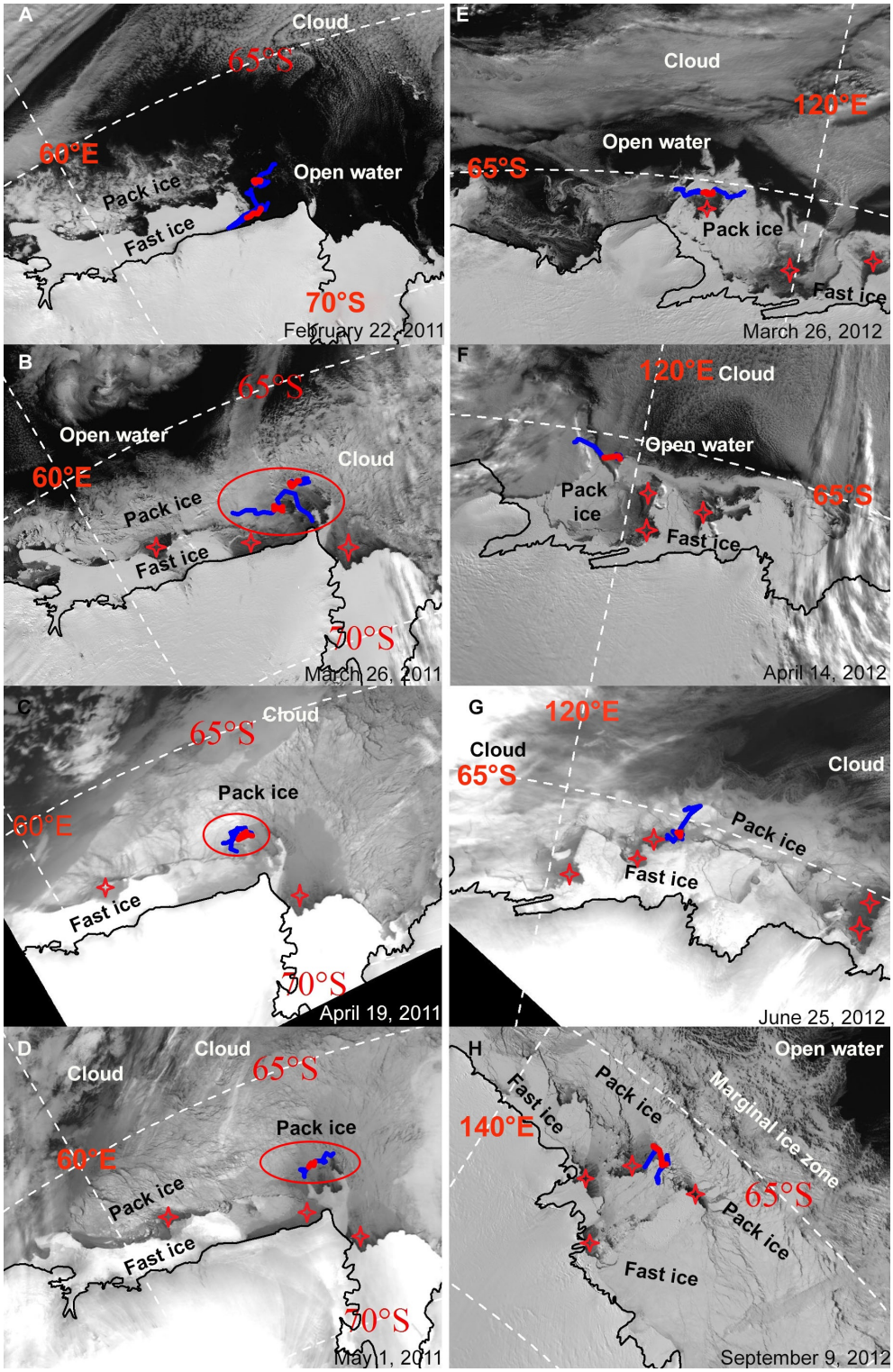


Figure III.11: Time-series of MODIS visible images of resolution 1 km illustrating male behaviour within sea ice from February to May 2011 within the region from 60 to 80°E (A-D) and from March to September 2012 within the region from 110 to 150°E (E-H). Coincident day animal track is represented by a red curve, while the blue part corresponds to the previous and subsequent two days. Polynyas and large open water areas are represented by red stars while red ellipses show where animals are within the Cape Darnley polynya.

Hindell et al. [Hindell et al., 2016] described the change in broad-scale habitat use of Kerguelen post-moult SESs throughout the year, with females moving northwards with the growth of the winter sea ice, and males remaining over the shelf. However, our study is the first to quantify the seasonality in foraging activity (in terms of time spent "hunting" during a dive) throughout winter. There was a clear increase in foraging activity for both males and females with a peak in later autumn/early winter and this will be discussed later.

For the first time, we investigated the importance of the spatio-temporal variability of sea ice during SES foraging trips, which is a key factor enabling them to exploit these ice covered regions, as suggested in Labrousse et al. [Labrousse et al., 2015]. Moreover, the regionally complex patterns in sea ice trends observed in East Antarctica over the past 30 years with local variability of the marine "icescape" [Massom et al., 2013] might allow the Kerguelen population to exploit concentrated sea ice patches or to remain deep in to the sea ice zone in polynyas areas. This contrasts with Macquarie Island where increasing sea ice extents in the western Ross Sea sector were negatively correlated with the number of breeding female SESs (with a lag of 3 years) presumably by limiting the access to profitable prey patches [van den Hoff et al., 2014]. Acting as an ecological double-edged sword, sea ice provides and concentrates a rich ecosystem during wintertime, while also representing a physical barrier for air breathing predators [Chambert et al., 2015]. Several studies based on emperor penguin already suggested an optimum level of ice cover with neither complete absence of sea ice nor heavy and persistent sea ice providing satisfactory conditions for sea ice dwelling species [Tynan et al., 2010, Barbraud et al., 2012, Jenouvrier et al., 2012].

The difference in the foraging areas visited by males and females is presumably explained by differences in energy requirements between juvenile males and adult females and the distribution of their prey [Bailleul et al., 2007a]. Small, schooling prey (e.g. Myctophids; [Cherel et al., 2008]) were likely to be targeted by seals foraging in pelagic waters, larger prey items such as Notothenids, Morids [Bradshaw et al., 2003, Banks et al., 2014] are probably more dominant prey items for seals foraging on the shelf while a mix of fish (Myctophids, Notothenids), squid and krill is probably found in the pack ice region [Banks et al., 2014, Walters et al., 2014].

This can also be explained by the timings of migration to and from the high latitudes; males in general arrive earlier than females on the shelf before sea ice forms probably allowing them to reach these remote areas without being constrained by sea ice. Moreover, males studied are sub-adult males, which may not prioritize returning to the colony for breeding as they may not be sexually mature and thus may be able to stay longer within the sea ice region. In contrast females arrive later when sea ice is already formed and leave earlier as they may prioritize returning to the colony to give birth. Thus females might avoid being trapped by sea ice by foraging in the pack but by following the sea ice edge [Bailleul et al., 2007a, Labrousse et al., 2015, Hindell et al., 2016]. Moreover, the ability to forage in sea ice may be related to body size. Males and larger females might use the sea ice zone more efficiently related to them being physically more capable of breaking through

the ice to breathe, and consequently being able to remain in these resource rich zones for longer [Hindell et al., 2016]. In our sample, a positive correlation between weight and females average distance from the edge was found.

Finally, sub-adult males may also be physically capable to escape predation from killer whales remaining in the pack ice or at the sea ice edge [Pitman, 2011], and may favour leads within fast ice or coastal polynyas to avoid predation.

Understanding these patterns requires also consideration of the resources available to the animals. We do this in the context of different sea ice zones, which might aggregate specific resources, as well as in the framework of the seasonal cycle in ice and primary production.

4.1 Sea ice zones and associated resources

In East Antarctica, the sea ice cover is made up of three zones with distinct characteristics [Massom and Stammerjohn, 2010]. These are (from north to south): i) the highly-dynamic "marginal ice zone" (MIZ), which typically extends 100 km or so south from the ice edge, and is generally made up of small floes and diffuse ice conditions (depending on wind direction); ii) the "inner pack ice" zone (PIZ) comprising larger floes separated by leads; and iii) a coastal zone comprising the band of compact “landfast (fast) ice” and persistent and recurrent areas of low-concentration sea ice in the form of polynyas and flaw leads. Females in our study mostly remained and foraged in the MIZ and the outer part of the pack ice, while males used all three sea ice zones. Below, we summarise female and male foraging behaviour in each of these zones in more detail.

Within the MIZ, both females and males encountered regions characterized by (i) relatively low to intermediate sea ice concentration; (ii) low $T_{80\%}$; and (iii) low to high $A_{80\%}$. The MIZ is characterized by high sea ice variability in time and space and enhanced biological activity due to sea ice melt and breakdown releasing an important quantity of food resources (i.e. ice algae) under a strong influence of wind action and ocean wave-ice interaction processes [Wadhams, 2000, Massom et al., 2006, Karnovsky et al., 2007, Squire, 2007, Massom and Stammerjohn, 2010]. However, it is not in this region that seals had the longest hunting times per dive.

Within the PIZ, females mostly remained in the outer part of the pack (150 – 370 km away from the edge) and had their longest hunting times there compared to the MIZ. Within this region, generally characterized by persistent and compact sea ice, females foraged most intensively (i) in the highest sea ice concentration at their position, but (ii) their hunting time was longer in areas of low concentration sea ice around their position (either in time or in space; 30 days and 50 km). The spatio-temporal variability of sea ice around female positions probably allowed them to exploit concentrated patches of prey without being trapped by the ice [Raymond et al., 2015].

Despite a lack of information on prey we hypothesize that females depend on energy derived from the primary production of algae growing in sea ice [Eicken, 1992, Van Franeker et al., 1997, Brierley and Thomas, 2002, Nicol, 2006, Clarke, 2008, Bluhm et al., 2010, Tynan et al., 2010]. Specifically, concentrated sea ice patches represent important habitat for krill and for the over-winter survival of juvenile krill [Frazer et al., 1997, Marschall, 1988, Massom and Stammerjohn, 2010, Schaafsma et al., 2016]. As algal biomass in sea ice is considerably greater than in the underlying water column in winter [Quetin and Ross, 2009], sea ice provides a key winter food source for dense swarms of krill (observations from remotely operated vehicles, [O'Brien, 1987, Marschall, 1988, Flores et al., 2012b]. In turn, krill supplies an under-ice ecosystem up to mesopelagic areas by transferring the energy to the pelagic food web through vertical migration, food chains and sinking detritus (reviewed by Brierley and Thomas [Brierley and Thomas, 2002]). While mesopelagic fish usually inhabit deep water in open water areas, in the pack ice areas some were found directly below sea ice (e.g. Antarctic lanternfish, [Kaufmann et al., 1995]; Antarctic silverfish, [Fuiman et al., 2002]; and cephalopods). Female elephant seals foraging in the PIZ made shallower dives than in other areas and sometimes performed dives shallower than 40 m. They may exploit these different prey directly under the sea ice or shallower than usual in the water column under pack ice. Indeed, females are known to have a multi-species diet, (i.e. mix of fish and squid) in the pack-ice habitat compared with shelf and pelagic habitats where females have a higher proportion of fish [Banks et al., 2014]. Evidence of a second major trophic pathway from phytoplankton to mesopredators in the pack ice region during autumn, via copepods and myctophids, comprised intermediate trophic steps via cephalopods and large fishes [Flores et al., 2008]. This suggests that the copepod – fish - top predator link is probably as important as the traditionally emphasized krill pathway especially for female SESs, known to favor highly energetic prey such as myctophids [Cherel et al., 2008] in mesopelagic layers. Thus, availability of resources near the surface in the pack ice region possibly makes it physiologically more rewarding to forage under-ice compared to the deep dives necessary to catch Myctophids in open waters or compared to the risk of being trapped by sea ice by foraging on Notothenids [Bradshaw et al., 2003] in densely sea ice covered shelf regions. Unfortunately, there is so far only anecdotal evidence that important prey species of SESs are found in the ice-water interface layer, such as squid and fish [Ainley et al., 1986, Kaufmann et al., 1995, Flores et al., 2011, David et al., 2016].

The pack ice region for males represents both a transit and a feeding area. However, male hunting time was longer in regions close to the Antarctic coast, in the southern part of the pack and fast ice (420 - 960 km away from the edge). Within this environment, they foraged most intensively (i) in the lowest sea ice concentration at their position, and (ii) their foraging activity was longer when there were more patches of low concentrated sea ice around their position (either in time or in space; 30 days and 50 km) likely to be associated with polynyas, or recurrent flaw leads separating persistent fast ice from moving pack ice [Massom and Stammerjohn, 2010]. In addition to relieving the sea ice con-

straints, these open water areas can sustain high biological activity. Polynyas often harbour large phytoplankton concentrations compared to surrounding ice-covered waters in early spring [Arrigo et al., 2015]. While these blooms happen between early spring and summer, Antarctic coastal polynyas are a site of concentrated biological activity with rich ecosystems that support large populations of mammals being able to breathe and feed throughout the ice season [Tynan et al., 2010, Arrigo and van Dijken, 2003, Karnovsky et al., 2007, Tremblay and Smith Jr., 2007, Arrigo et al., 2015]. Polynyas also support rich benthic communities through enhanced vertical carbon flux [Grebmeier and Barry, 2007]. Juvenile male SESs may also benefit from this by feeding on the shelf or slope regions without being constrained by sea ice. They likely feed on the most abundant pelagic fish in Antarctic shelf water, the Antarctic silverfish (*Pleuragramma antarcticum*), from surface to ~ 900m [Daneri and Carlini, 2002, La Mesa et al., 2010] or on epibenthic Antarctic toothfish (*Dissostichus mawsoni*) [Bradshaw et al., 2003, Smith et al., 2007] with juvenile fish principally found on the shelf while adults are found along the slope [Ashford et al., 2012] sometimes shallower than though within ~ 1000 m of the water column [Watwood et al., 2006] or under fast ice in mid-depths [Fuiman et al., 2002]. Shallow dives observed in high sea ice concentration close to the Antarctic coast could correspond to specific foraging activity associated with the rich under-ice community of fish and invertebrates [Ainley et al., 1991]. Moreover, these dives were mostly performed at night, where the diurnal vertical migration of adult krill (*Euphausia crystallorophias*), more pronounced in winter than summer [Siegel, 2012, Flores et al., 2012b] might attract various preys, such as Pleuragramma antarcticum [Fuiman et al., 2002].

4.2 Seasonality in foraging activity

Our analysis highlights the importance of the seasonal cycle to the seal hunting time. For both males and females, we found that hunting time per dive increased from April to June. This is not surprising given that sea ice characteristics are intrinsically related to seasons, but whether the season itself (i.e. productivity of the ecosystem at a certain period) or seasonal changes in along-track sea ice habitat (i.e. access to favorable zones with prey availability later in the season) that affect seal foraging behaviour remains open to question.

When we considered the importance of $A_{80\%}$ on the hunting time, we found that both males and females favored high values of$A_{80\%}$. However, season was highly correlated with this variable. Is this result just reflecting that hunting time increases later on the season to fulfil ecological and/or physiological requirements or is it linked with changes in resources availability associated with high values of $A_{80\%}$? In an attempt to answer this question, we considered the anomaly (from its seasonal cycle) of the sea ice cover around seal position ($A'_{80\%}$). We found that years with positive values of $A'_{80\%}$ were associated with shorter hunting times. We therefore speculate that the season is key to understanding seal hunting time, with longest hunting time associated with autumn. And, within a given season, both males and females hunt longer when they were more patches of low concentrated sea ice around

their position, which might provide to the animals easier access to air for breathing and therefore easier environment to hunt. Thus, to answer the previous question, increased hunting times were not linked with high values of $A_{80\%}$.

The under-ice ocean seasonal cycle is characterized by the presence of an autumn (May–June) bloom in sea ice [Fritsen et al., 1994, Lieser et al., 2015]. Based on our previous hypothesis that the season itself affects foraging behaviour, we conclude that such an autumn bloom could affect hunting time through ecosystem cascades. Ice algal autumn blooms are generally not intense, but they are biologically significant and could provide a readily accessible food source for pelagic herbivores such as krill, which may in turn sustain upper trophic levels in autumn/early winter season [Meiners et al., 2012]. Regarding polynyas, primary production in early spring/summer appears to extend feeding and reproduction in zooplankton (such as copepods and euphausiids) into late summer and early autumn [Deibel and Daly, 2007]. Similarly, middle to upper trophic levels might benefit from this secondary production and concentrated resources through the autumn/early winter season.

Finally, buoyancy of the seal may also play a role in the positive correlation between hunting time and season. At the start of post-moult foraging trips, SESs are negatively buoyant, but along their trip, when they acquire resources and get fatter, they get closer to the neutral buoyancy (a critical factor of the swimming effort). It was found by Jouma'a et al. [Jouma'a et al., 2016] that the closer the seal was to neutral buoyancy the longer was the bottom duration, and consequently the hunting time.

5 Conclusion

Understanding the linkages between predators and sea ice is essential to any attempt to make robust and reliable predictions about ecosystem responses to future climate related sea ice change. For "non sea ice obligate species" such as SESs, the importance of sea ice patterns along their winter foraging trips are not well understood. It is known, however, that high-latitude marine ecosystems exploited by SESs are extensively influenced by the presence, seasonal rhythms and properties of sea ice [Massom and Stammerjohn, 2010]. Here, we have confirmed important associations between seal foraging behaviour and sea ice, and we brought new insights on the role of the spatio-temporal variability of sea ice along their tracks. It builds upon previous studies that the responses of predators to sea ice and its variability are complex, involving aspects of seasonality and position within sea ice. Females had longer hunting times in the outer pack ice in concentrated sea ice patches but the spatio-temporal variability of sea ice around female positions is probably a key factor allowing them to exploit these ice covered regions. Males had a different strategy: they used polynyas and open water areas deep inside the pack on the shelf. This suggests that the ecosystems developing at the ice-water interface might play a crucial role in sustaining the predator populations in the Antarctic seasonal sea ice zone (e.g. winter foraging trips of Emperor penguins, [Kirkwood and Robertson, 1997a, Ponganis et al., 2000].

Our understanding of the complex linkages between sea ice and ecosystems still remains limited by restricted ship access, difficulties in sampling in remote environments during wintertime, and the patchiness of biota at any given location [Brierley and Thomas, 2002, Steffens et al., 2006]. In addition, our understanding of the trophic ecology of benthic and mesopelagic communities within the sea ice region that SESs consume is extremely limited [Costa et al., 2010]. Resource limitation due to low primary productivity in winter is often regarded as a key factor, however, we show in the present study that food consumption of the top predator community such as SESs persists or increases hundreds of kilometres deep into the pack ice (see also [Van Franeker et al., 1997, Flores et al., 2012b]). An underestimate by pelagic sampling in the past may have caused ice-covered areas to appear poorer in biological resources than they really are [Flores et al., 2012b]. Moreover, the current neglect of an autumn bloom from non-detection of ice-associated phytoplankton in conventional satellite ocean-colour images may have also underestimate the potential of sea ice to sustain a rich under-ice ecosystem during winter [Lieser et al., 2015]. Thus this work also contributes to deepening our knowledge on (i) the functioning of the under-ice biological habitat and (ii) ecological mechanisms that take place in remote and extreme environments with limited access.

The continued sustained monitoring of vertebrate colonies relative to sea ice parameters around the Antarctic coast and islands is crucial, given the complexity of the impact of climate forcing on biotic and abiotic components of the Antarctic marine ecosystem [Clarke, 2008, Massom and Stammerjohn, 2010].

Acknowledgements

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and volunteers involved in the research on southern elephant seals in Kerguelen. All animals in this study were treated in accordance with the IPEV ethical and Polar Environment Committees guidelines.

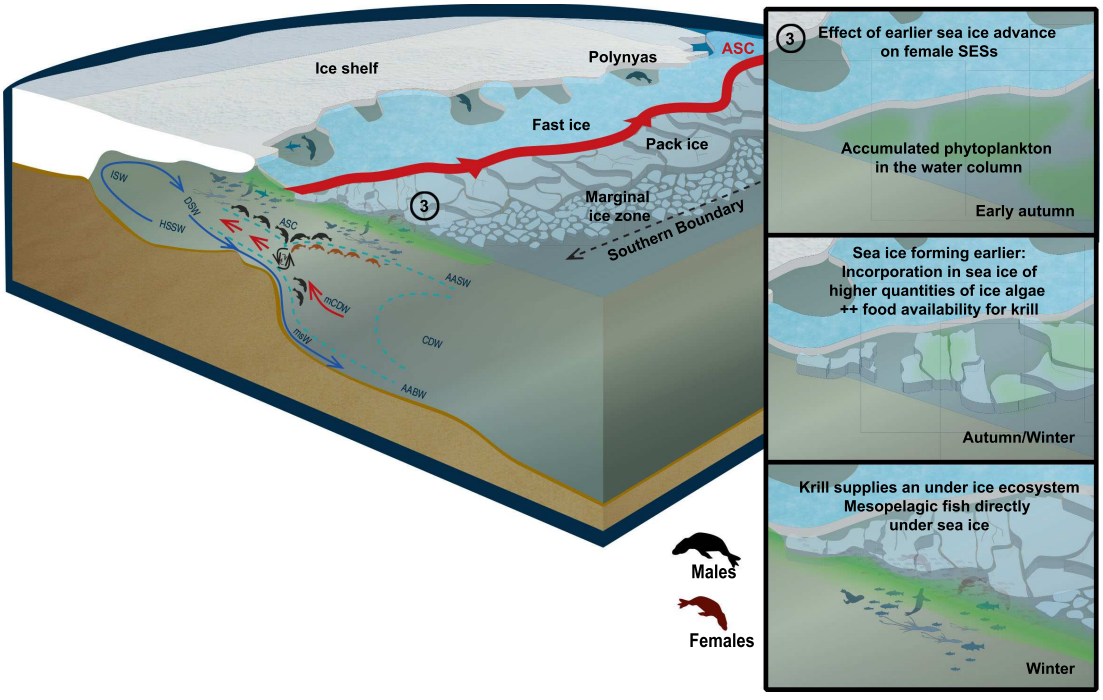
CHAPTER

IV

Variability in sea ice cover and climate elicit sex specific responses in an Antarctic predator

This chapter is under review as *Variability in sea ice cover and climate elicit sex specific responses in an Antarctic predator* by S. Labrousse, J-B. Sallée, A.D. Fraser, R.A. Massom, P. Reid, W. Hobbs, C. Guinet, R. Harcourt, C. McMahon, F. Bailleul, M.A. Hindell and J-B. Charrassin in ***Scientific Reports***, 2016.

Schematic of the results from chapter IV. Refer to the general discussion 5 for detailed caption.



The pattern of change in sea ice seasonality off East Antarctica over the last three decades are mixed, with contrasting signals at regional scales. I thus found it important to change the scale of analysis to investigate how medium term changes in sea ice would affect seal foraging behaviour over an 11 year time-series. This is a step towards the understanding of how seal may adapt to future environmental changes. In this chapter, we focused on if and (if so) how the interannual variability of sea ice cover and dynamics effect seal foraging behaviour. We also proposed mechanisms by which climate forcing affects both abiotic and biotic components of the Antarctic marine ecosystem, and in turn mesopredators through trophic cascading processes. This is a second step in our understanding of the direct and indirect linkages between sea ice conditions and seal foraging behaviour and movements.

Abstract

Contrasting regional changes in Southern Ocean sea ice have occurred over the last 30 years with distinct regional effects on ecosystem structure and function. Quantifying how Antarctic predators respond to such changes provides the context for predicting how climate variability/change will affect these assemblages into the future. Over an 11 year time-series, we examine how inter-annual variability in sea ice concentration and advance affect the foraging behaviour of a top Antarctic predator, the southern elephant seal. Females foraged longer in pack ice in years with greatest sea ice concentration and earliest sea ice advance, while males foraged longer in polynyas in years of lowest sea ice concentration. There was a positive relationship between near-surface meridional wind anomalies and female foraging effort, but not for males. This study reveals the complexities of foraging responses to climate forcing by a poleward migratory predator through varying sea ice property and dynamic anomalies.

1 Introduction

Over the last 30 years, Earth's polar regions have experienced significant changes in their sea ice coverage, with predictions of accelerated future change in the coming century [IPCC, 2014]. The Southern Ocean has already undergone large regionally-contrasting trends in sea ice coverage over the last 30 years. This is characterized by gain in the Ross Sea and loss in the neighbouring Amundsen/Bellingshausen Seas sectors [Parkinson and Cavalieri, 2012, Stammerjohn et al., 2012], with patterns of change/variability across the extensive East Antarctic sector being more spatially complex [Massom et al., 2013]. Sea ice-covered regions represent a unique and highly productive habitat and in the face of these large changes, ice coupled ecosystems experience re-organization associated with rapid change of their habitat [Massom and Stammerjohn, 2010]. Change in ecosystem structure and function may translate into modification of top predator population dynamics, because top predators integrate the spatio-temporal variations in underlying trophic levels [Hindell et al., 2003a].

Long-term studies have recently started to quantify the relationships between top predator population dynamics and inter-annual variability in sea ice concentration and extent (e.g. refs [Barbraud and Weimerskirch, 2006, Proffitt et al., 2007, Siniff et al., 2008, Massom et al., 2009, Trivelpiece et al., 2011, Forcada et al., 2012, Jenouvrier et al., 2012, van den Hoff et al., 2014, Southwell et al., 2015]). Responses observed are not uniform among populations and species around Antarctica [Massom and Stammerjohn, 2010], yet much remains to be understood about how individual animals use their environment, and how both environmental and associated food-web changes, effect their foraging performance at-sea, and ultimately their population dynamics. In this study, we can address this as we have collected a unique 11-year time series of coupled sea-ice and seal behavioural observations. We present novel results on the foraging behaviour of southern elephant seals (SESs) according to regional variability in sea ice and wind patterns across East Antarctica.

SESs are deep-diving, wide-ranging predators [Hindell et al., 1991b], and major consumers of marine resources of the Southern Ocean [Guinet et al., 1996, Hindell et al., 2003b], they depend upon an extensive set of trophic levels within the marine food web. They utilize different marine habitats depending on their sex [Bailleul et al., 2010a, Labrousse et al., 2015] and their breeding colony locations [Hindell et al., 2016]. For these reasons, SESs are unique model species to investigate physical changes over wide spatio-temporal ranges and they provide an unprecedented opportunity to integrate behaviour and physical structure to quantify how animals respond to variation in their environment. As a non sea ice-obligate species, SESs are often under-represented in ecological sea ice studies yet they strongly interact with sea ice during their Antarctic foraging trips [Bornemann et al., 2000, Bailleul et al., 2007a, Biuw et al., 2010, Labrousse et al., 2015, Hindell et al., 2016]. The under-ice environment supports a rich winter food resource, providing both a substrate for the growth of ice algae and a refuge for herbivorous zooplankton such as juvenile krill and other crustaceans [Marschall, 1988, Massom et al., 2006, Flores et al., 2012b, David et al., 2016], which in turn attracts higher trophic levels such as pelagic fish and their predators [Eicken, 1992, Reid and Croxall, 2001, Brierley and Thomas, 2002, Fraser and Hofmann, 2003, Tynan et al., 2010]. Inter-annual changes in both regional sea ice concentration and the timing of sea ice advance may therefore affect the availability of resources within the sea ice zone [Massom and Stammerjohn, 2010], but no studies have assessed the foraging response of diving predators to such change/variability.

Around much of Antarctica, variability in sea ice concentration and the timing of annual sea ice advance (and retreat) is linked with variability in wind patterns as they affect both sea ice dynamic and thermodynamic processes. While cold southerly winds tend to drive enhanced equatorward ice advance and (depending on the season) increase the ice concentration, warmer northerly winds can compact the sea ice [Liu et al., 2004, Lefebvre and Goosse, 2005, Massom et al., 2008, Turner et al., 2009, Holland and Kwok, 2012]. In East Antarctica, recent analyses have

shown that changes in sea ice contain a strong wind-driven thermodynamic component [Holland and Kwok, 2012]. Coupled sea ice model experiments depict a strong, non-annular response of wind-induced sea ice drift in East Antarctica, with strong westerlies leading to increased sea ice concentration in the western part of this region while further east, a strong northerly wind results in decreased sea ice concentration [Deb et al., 2016]. Aspects of these winds and sea ice changes are associated with trends in large-scale climate modes of variability such as the Southern Annular Mode (SAM) [Liu et al., 2004, Stammerjohn et al., 2008, Yuan and Li, 2008, Deb et al., 2016], which itself is forced by the Southern Hemisphere ozone hole and increased greenhouse gases [Turner et al., 2009, Gillett et al., 2013].

In this study, we examine an 11-year time-series (2004-2014) of SES movements and diving behaviour to quantify how wind variability and the associated sea ice variability, both forced by large-scale climate variability, affect top predator foraging activity through abiotic and biotic mechanisms. Previous work on this dataset has shown that adult females prefer to forage in high sea ice concentration regions, close to the sea ice edge in the pack ice, while juvenile males remain deep within the sea ice to forage mainly over the Antarctic shelf or within the Antarctic Slope Front and in low sea ice concentration regions (presumably polynya areas) [Bailleul et al., 2007a, Labrousse et al., 2015, Hindell et al., 2016]. In the present paper, we show for the first time how this sex-dependent habitat utilization is affected by inter-annual variability in sea ice in East Antarctica. In particular, we highlight the role of near-surface meridional winds, incorporating large-scale climatic variability, in impacting predators through their effects on regional sea ice changes. The effect of the timing of sea ice advance on seal foraging performance brings new insights to the underlying seasonal trophic mechanisms by which sea ice is critical to Antarctic ecosystems right through to predators.

2 Method

2.1 Animal handling, deployment, data collected and filtering

We use location and dive depth data from 43 post-moulting SESs (21 females and 22 males) that were instrumented with CTD-SRDLs (Sea Mammal Research Unit, University of St Andrews) between December and February in 2004, 2008-2009 and 2011-2014 on the Kerguelen Islands (49°20'S, 70°20'E) (Appendix C, Table CX1). These animals were chosen from a larger dataset because they visited the area south of 55°S (the spatial domain for the study), which is equivalent to the maximum latitude of annual sea ice extent (in September). Unusual behaviour was observed in five animals (two females and three males) that returned to the colony before heading back to sea again. For these individuals, the section of the tracks where the animals travelled south within the sea ice region (one female and two males) after their return to the colony were removed from the analysis. Details of the instrumentation, seal handling and data processing for dives and filtering ARGOS positions

are provided in ref. [Labrousse et al., 2015]. All animals in this study were handled in accordance with the French Polar Institute (Institut Paul Emile Victor, IPEV) ethical and Polar Environment Committees guidelines associated with the research project IPEV 109 (PI H. Weimerskirch). The experimental bio-logging protocol was approved by the IPEV ethical and Polar Environment Committees.

2.2 Foraging activity

Foraging activity of each seal was analysed at the dive scale using the methodology developed by ref. [Heerah et al., 2015], which estimates the time spent hunting during a dive. For each dive, the time spent in segments with a vertical velocity lower or equal to 0.4 $m.s^{-1}$ was calculated. This time was termed hunting time per dive and was used as a proxy for foraging activity.

2.3 Sea ice concentration anomalies

SSMI/S daily sea ice concentration (resolution 25 km) provided a continuous time-series for the years of the study. The mean seasonal cycle of sea ice concentration was produced by averaging daily maps corresponding to the same day of year, over the 11 years of the study. Once the seasonal cycle was computed from this time series, we then removed this signal from the time series of sea ice concentration, to create an anomaly from the local seasonal cycle.

In order to test relationships between daily sea ice concentration anomalies and seal hunting times, we grouped all seal hunting times corresponding to the location of anomalously negative and positive sea ice concentrations (defined as a sea ice concentration anomaly lower or greater than one standard deviation of sea ice concentration anomaly respectively). For this calculation, we only considered seals inside the sea ice region (as defined by their distance to the sea ice edge, i.e. 15% ice concentration isoline) and from March onward, as previously defined. We then compared the two distributions of hunting times using a permutation test (bootstrap analysis) [Good, 2005]. We repeated the experiment of grouping seals hunting time 10,000 times, but randomly selected seals in our dataset, i.e. independent of collocated sea ice concentration anomalies. We then compared the distribution of the 10,000 differences in hunting time from the 10,000 random pairs of groups, to the difference of hunting time from the two groups based on sea ice concentration anomalies. Finally, SSMI/S monthly sea ice concentration (resolution 25 km) were used to compute monthly sea ice concentration anomalies to perform the correlation with monthly wind anomalies (see section Surface wind anomalies).

2.4 Sea ice advance anomalies

The day at which sea ice advances in the season (hereafter referred to as sea ice advance) was derived following ref. [Massom et al., 2013] using the NASA Bootstrap SMMR-SSM/I NASA Team combined dataset of daily sea ice concentration64 (http://nsidc.org/data/nsidc-0051.html) with a resolution of 25 km. Following ref. [Stammerjohn et al., 2008], the day of ice advance is taken to be the time at which sea ice concentration in a given pixel first exceeds 15% (proxy for the ice edge) for at least 5 consecutive days, for a given sea ice year (twelve months from mid-February). We computed the sea ice advance anomalies (from the local seasonal cycle) by removing the local climatological seasonal cycle computed over the 11 years of the study. We then collocated the sea ice advance anomalies at each seal position and time.

The goal of computing sea ice advance anomalies was to determine any possible influence of relatively early or late sea ice advance on seal foraging behaviour. The period during which seal hunting behaviour is likely to be affected by an earlier or later sea ice advance would be around the time of year at which sea ice usually advances. We therefore only selected seals' positions during the seasonal advance of sea ice from March to June65 that occurred within a 30-day window around the day of sea ice advance for a given year and at a given pixel. From this sub-sample, we compared the hunting time distribution for the two groups of seals i.e., those associated with later advance (i.e. positive anomalies), and those with earlier advance (i.e. negative anomalies). Similar to the sea ice concentration anomaly procedure, we estimated the significance of the difference in hunting time for the two groups using a permutation test.

2.5 Surface wind anomalies

Surface zonal and meridional winds were extracted from monthly ERA-Interim 10 m atmospheric reanalysis (http://apps.ecmwf.int/datasets/) with a spatial resolution of approximately 80 km. We computed meridional wind anomalies (from the local seasonal cycle) by removing the local climatological seasonal cycle computed over the 11 years of the study. The relationship between monthly meridional wind anomalies and monthly sea ice concentration anomalies was likely to be non-linear, so the correlation for each longitude/latitude pixel over the 11 year time period was performed using a Spearman correlation. For both variables, the periodic inter-annual variability was taken into account and the first trend in the anomalies was removed prior to correlation. The relationship between monthly meridional wind anomalies and sea ice advance anomalies was processed in three steps: (i) for each 5° longitude bin, monthly ERA-Interim 10 m wind anomalies were averaged within the minimum and maximum latitude band of average day of advance from 2004 to 2014; then (ii) the resulting averaged winds per month for each 5° longitude were averaged from March to June to obtain one-yearly data per bin of longitude; and finally (iii) a Spearman correlation between sea ice advance anomalies and averaged wind anomalies for each 5° bin of longitude was computed.

2.6 Statistical modelling

A Gaussian additive mixed effects model (GAMM) was fitted to examine the statistical relationships between seal foraging activity (expressed by the hunting time per dive) and the 10 m wind anomaly meridional component data. Based on the GAMM outcome, we then fitted a linear mixed effects model (LMM). Monthly ERA-Interim 10 m wind anomalies were collocated at each seal position and time. A subset of the data was extracted to only focus on parts of the tracks influenced by sea ice; for this, only positions inside the sea ice and from March (when the seasonal signal of sea ice concentration starts to increase [Raphael and Hobbs, 2014]) to the end of the post-moult trip were used for subsequent analysis. For each individual within a given month, hunting times per dive and monthly 10 m wind collocated at the seal dive position were averaged monthly. Models were computed with the R packages *mgcv* and *nlme* (from R Development Core Team, function *gamm* and *lme*) using restricted maximum likelihood. The response variable was centred and scaled for each seal prior to analysis to correct for non-Gaussian distribution. Outliers in the variables were checked. Sex was included in the model as an interaction factor variable. We first determined the optimal structure by assessing if individual seals as a random intercept term contributed to the model fit. The final model was then fitted using restricted maximum likelihood (REML). Model validation was checked by plotting Pearson residuals against fitted values, and against the explanatory variable, to verify homogeneity and normality of residuals [Zuur et al., 2010]. Finally, a marginal R-squared (i.e. variance explained by fixed factors only) and a conditional R-Squared (i.e. variance explained by both fixed and random factors) were calculated using the R package *MuMIn* (from R Development Core Team, function *r.squaredGLMM*).

3 Results

3.1 Seal foraging strategy and sea ice habitat

Winter post-moult foraging trips of 43 SESs (21 females and 22 males for a total of 273,542 dives) from Kerguelen Islands to the seasonal Antarctic sea ice zone were monitored using satellite-relayed position and diving data from 2004 to 2014 (Figure IV.1; see also Appendix C, Table CX1). Previously we identified two foraging strategies among post-moult Kerguelen SESs: open ocean foragers that predominantly use the Kerguelen shelf or frontal regions of the Antarctic Circumpolar Current (ACC), and high Antarctic specialists that forage mainly in the sea ice covered seas in close proximity to the Antarctic continent [Bailleul et al., 2010a, Hindell et al., 2016]. In this study we focus on the latter group of seals.

The tracked seals spanned a large region longitudinally ranging from 0 to 150°E (Figure IV.1), which can be divided into three sectors with distinct sea ice cover characteristics [Massom et al., 2013]: (i) from 0 to 50°E, the winter sea ice cover has a large latitudinal range relatively early in the season (before March/April),

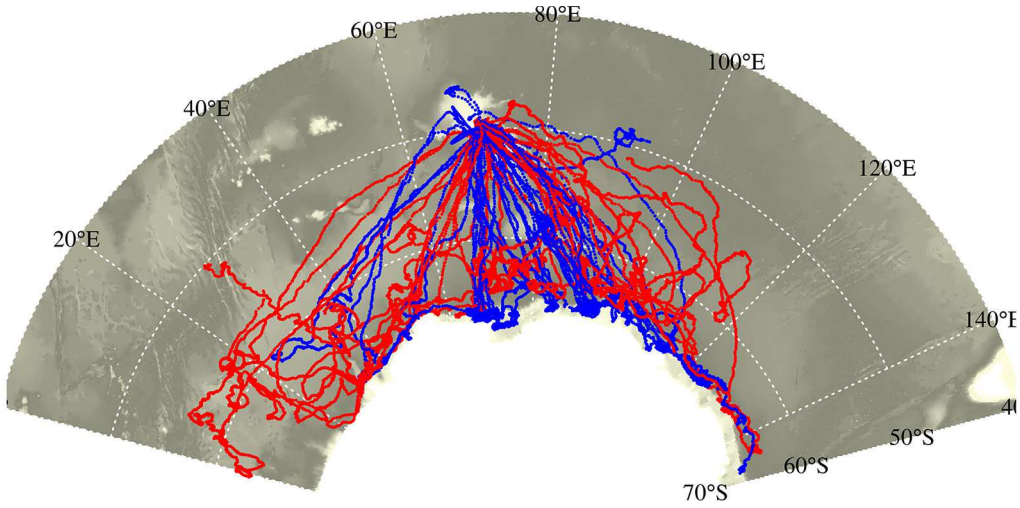


Figure IV.1: Tracks of the 43 southern elephant seals equipped with CTD-SRDLs from 2004 to 2014. Their movements and diving behaviour were collected during their post-moult foraging trip from the breeding colony in Kerguelen Islands to the Antarctic sea ice zone. Red and blue colours represent the 21 females and 22 males, respectively. The map was made using R software, version 3.2.4 revised (R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/). The bathymetry represented in grey shading is from The GEBCO_08 Grid, a global 30 arc-second grid largely generated by combining quality-controlled ship depth soundings with interpolation between sounding points guided by satellite-derived gravity data. URL http://www.gebco.net/data_and_products/gridded_bathymetry_data/.

largely driven by net sea ice production within sea ice and at the sea ice edge [Kimura and Wakatsuchi, 2011a] and supplemented by an eastward transport of sea ice from strong westerlies (during positive SAM events)[Deb et al., 2016] and within the eastern Weddell Gyre [Kimura and Wakatsuchi, 2011a]; (ii) from 50 to 90°E, the sea ice cover also extends far to the north, with a number of coastal polynyas producing large amounts of sea ice [Tamura and Ohshima, 2011] which is transported offshore by a net northward winds and the Prydz Bay Gyre, both within the climatological low-pressure Amery Bay region [Deb et al., 2016]; and (iii) from 90 to 150°E, a narrower zone of sea ice which is mostly fed by production in coastal polynyas and leads and supplemented by advection (input) from the east [Kimura and Wakatsuchi, 2011a, Massom et al., 2013]. Wind convergence (i.e. stronger northerly wind component during positive SAM events) in the eastern part can locally limit the sea ice extent resulting in compacting ice at the coast [Massom et al., 2008, Deb et al., 2016].

The figure IV.2 illustrates the averaged sea ice cover, advance and near-surface wind patterns from 2004 to 2014 during the winter season for the study region. In each of sectors described above, the mean wind field is consistent with the mean sea ice cover and day of advance. We also observed in figure IV.2 the processes described above: concentrated sea ice and advance extending far north due to the eastward transport of sea ice in the first

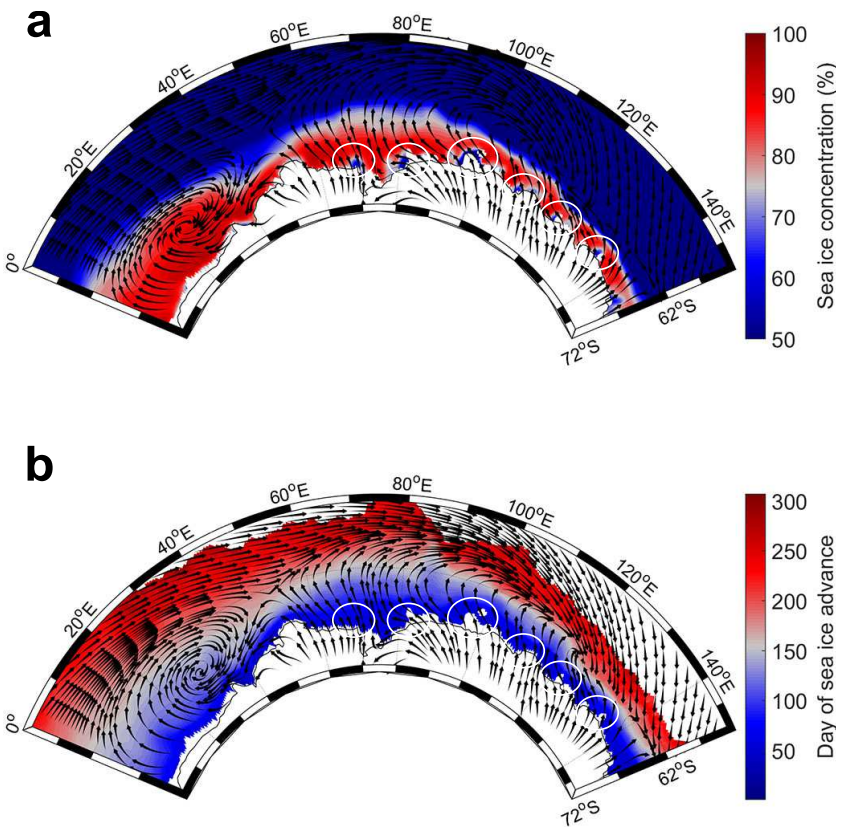


Figure IV.2: Climatological patterns of sea ice and near-surface winds from 2004 to 2014. (**a**) Mean sea ice concentration (expressed as percentage) and monthly-averaged ERA-Interim 10 m winds zonal and meridional component are shown for the winter season (June-August). (**b**) Mean day of sea ice advance and monthly-averaged ERA-Interim 10 m winds zonal and meridional component from March to June. Ellipses represent coastal polynya sites, from left to right: Cape Darnley/Mackenzie, Barrier, Shackleton, Vincennes Bay, Dalton, and Dibble. For illustration purposes, autumn-averaged sea ice concentration (March-May) is not represented. Maps were made using MATLAB software (version 8.5.0.197613 (R2015a), URL http://fr.mathworks.com/).

sector and to net northward winds in the second sector; a narrow sea ice zone due to wind convergence in the third sector; and generally over the whole study region stronger mean northward wind driving earlier sea ice advance in the pack ice region.

3.2 Seal foraging activity response to inter-annual sea ice cover anomaly

The mean sea ice concentration and day of sea ice advance exhibit large inter-annual variability across East Antarctica [Massom et al., 2013]. To investigate how seals respond to this, we divided the individual dives into two groups; those foraging during strongly positive and negative sea ice concentration anomalies, for both males and females (see Methods section 2.3). The combined number of seal observations in the two groups of sea ice concentration anomalies comprised about 9% of the total female dives (n = 12,694 dives) and 12% of the total male dives (n = 15,996 dives). Similarly, we defined two further groups of dives corresponding to earlier or later sea ice advance (as opposed to concentration), for both males

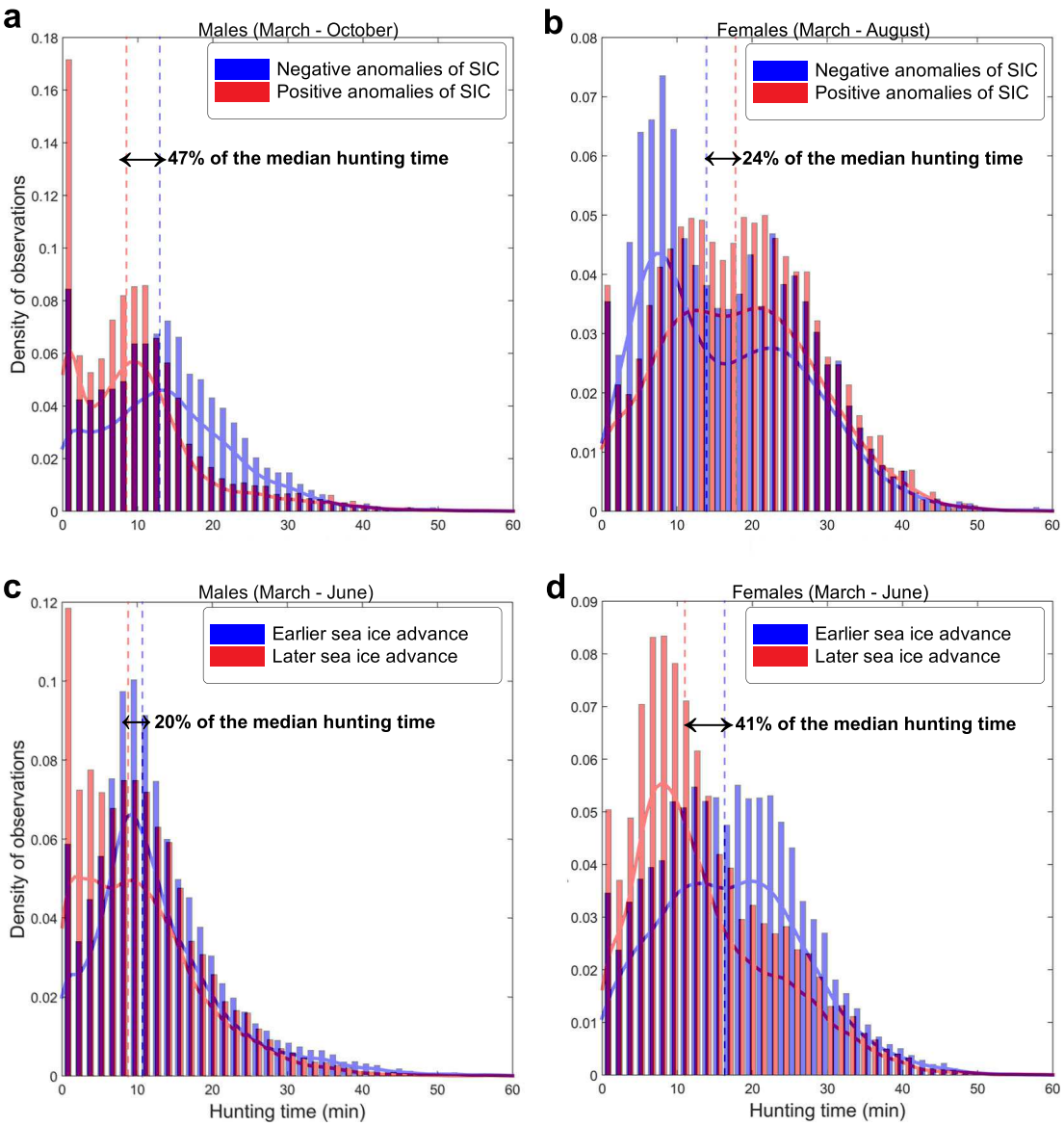


Figure IV.3: Influence of sea ice changes on male and female foraging activity from 2004 to 2014. Normalized histograms of the sum of observations in each bin of hunting time (i.e. a proxy of seal foraging activity expressed in minutes) are represented for negative or positive sea ice concentration anomalies (see Methods) for (**a**) males and (**b**) females. The same histograms are presented for earlier and later advance of sea ice for (**c**) males and (**d**) females. For each group of anomalies, the probability density function was superimposed and the dashed lines represent the median hunting time for each group of anomalies for males and females. Please note that hunting times equal to 0 were removed for illustration purposes.

and females (see Methods section 2.4). The combined number of seal observations in the two groups of sea ice advance anomaly was 58,906 dives, comprising about 25% of the total female dives (n = 35,038) and about 18% of the total male dives (n = 23,868).

For males, hunting times were on average 4.6 min/dive longer (or 47% of the median hunting time) when sea-ice concentration was lower (negative) than when positive sea ice concentration anomalies were observed (Figure IV.3a). The maximum difference in hunting times between two generated random groups of sea ice concentration anomalies from the bootstrap analysis was 0.6 min/dive, i.e. ~ 8 times lower than the test condition (p-value ~ 0), confirming the significance of negative sea ice concentration anomalies in influencing male hunting times. Hunting times were 1.9 min/dive longer (or 20% of the median hunting time; Figure IV.3c) in years with earlier sea ice advance. Using a bootstrap analysis, the maximum difference in hunting times between two generated random groups of earlier and later sea ice advance was 0.5 min/dive, i.e. ~ 4 times lower than the test condition. Thus, the difference between earlier and later sea ice advance was significant (p-value ~ 0) but the impact of earlier sea ice advance for males was relatively low.

In contrast to males, positive sea ice concentration anomalies were associated with longer hunting times for females (i.e. 3.9 min/dive longer or 24% of the median female hunting time; Figure IV.3b). The bootstrap analysis showed a maximum difference in hunting times of 1.3 min/dive, i.e. ~3 times lower than the test condition. While the difference between sea ice concentration anomalies was significant (p-value ~ 0), the impact of sea ice concentration anomalies on female hunting times was less important than for males. However, the effect of earlier sea ice advance on female hunting times was more marked, with their foraging time increasing by ~ 5.3 min/dive, i.e. 41% of the median hunting time (Figure IV.3d). Bootstrap analysis confirmed this result for females: the maximum hunting time differences in median for randomly chosen groups of earlier and later advance was 0.6 min/dive, i.e. 9 times lower than the test condition, confirming the significance (p-value ~ 0).

3.3 Inter-annual sea ice cover anomaly response to anomalous winds

Both the local anomalies of sea ice concentration and advance effected seal foraging activity, with the ice anomalies being (at least partly) controlled by local near-surface winds [Liu et al., 2004, Lefebvre et al., 2004, Turner et al., 2009, Holland and Kwok, 2012, Deb et al., 2016]. Indeed, the correlation between local sea ice concentration and local winds anomalies (which are defined as deviation from mean seasonal cycle) over the time period examined (2004-2014) shows clearly differing wind-sea ice relationships across the different sectors of our study region (Figure IV.4a). In the westernmost (0–50°E) and easternmost (90–150°E) sectors, significant positive correlations were found between near-surface northward wind and sea ice concentration anomalies in the ice-covered region (Figure IV.4a). By contrast, in the intervening sector extending from 50°E and 90°E, there were significant negative correlations between sea ice concentration and near-surface northward wind anomalies. The largest negative correlation in this sector was found around the Mawson Coast/western Prydz Bay (60 – 75°E, Figure IV.4a). This negative correlation suggests strong offshore transport of sea ice newly formed within the coastal polynyas. A

similar and consistent impact of northward winds was also found for the day of sea ice advance (Figure IV.4b). Negative correlations were found in the westernmost (0–50°E) and easternmost (90–150°E) sectors, with an increase in the northward component of the near-surface wind being associated with earlier sea ice advance. This contrasts with observations in the 60 – 75°E sector, where the larger the northward component of near-surface wind, the later the sea ice advance. This latter was presumably because of efficient zonal export of the early-formed sea ice, preventing sea ice from accumulating locally leading to later sea ice advance. These relationships were also found in all coastal polynyas (Figure IV.4a). However, the presence of thin ice early in the season or multi-year sea ice in polynyas may lead to artefacts in the calculation of sea ice concentration and advance and consequently misinterpretation of the observed correlation.

3.4 Indirect influence of local wind anomalies onto seal foraging activity

Our observations suggest that seal foraging activity is influenced by inter-annual sea ice anomalies, which are themselves a product of wind anomalies. Therefore we now investigate whether there is an indirect influence of wind on seal foraging activity. A linear mixed effects model (see Methods section 2.6) was used to investigate the relationship between wind anomalies and seal foraging activity. We found that there was a positive relationship (t-value = 4.4, p-value = 0) between the near-surface meridional wind anomalies and female hunting times, but not for male hunting times (t-value = -0.52, p-value = 0.6; Figure IV.5). Linking hunting times at the dive scale (monthly averaged per individual) with monthly wind anomalies (monthly averaged per individual) at a coarse spatial resolution of approximately 80 km is appropriate as wind-driven sea ice changes occur at larger spatio-temporal scales than the dive scale. However, this also means that the present analysis presumably captures the global influence of wind on seal foraging activity through sea ice changes but not local changes in hunting times, and this may explain the relatively weak relationship (marginal R-squared of 12.5%).

4 Discussion

Favourable conditions for female foraging activity (i.e. longer hunting times) were observed for years of increased sea ice concentrations and earlier sea ice advance. We hypothesize that the early development and advance of sea ice in autumn would enhance primary production within the ice [Quetin and Ross, 2009, Massom and Stammerjohn, 2010] thereby providing increased resources for predators within the ice in winter (through different trophic cascading effects). Timing of ice formation is critical in at least two ways: (i) an early ice formation could result in incorporation of more phytoplankton from fall blooms into the ice, (ii) more total light available for ice algal growth before mid-winter (Figure 6a; see ref. [Raymond et al., 2009]). Thus, ice forming earlier would have higher concentrations of ice algae than later-forming ice, resulting in higher krill growth

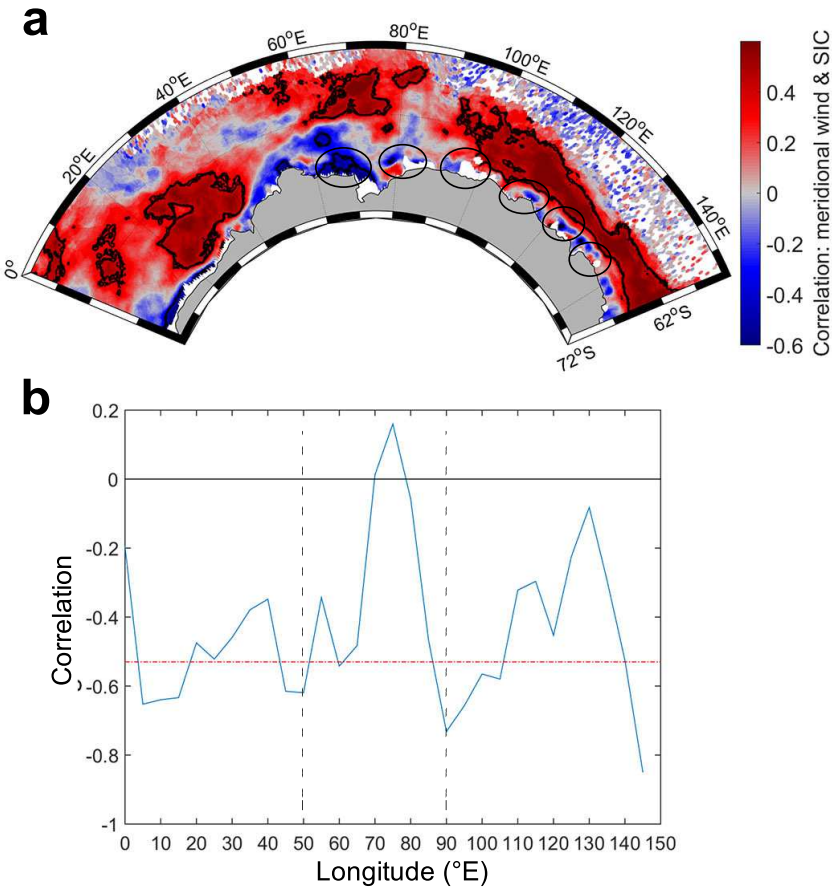


Figure IV.4: Relationship between 10 m wind meridional component and sea ice patterns from 2004 to 2014. Per-pixel Spearman correlation coefficient between monthly ERA-Interim 10 m wind meridional component anomaly and monthly sea ice concentration anomalies from 2004 to 2014 is represented for the winter season (June-August), with contours denoting statistical significance at the 95% level. Ellipses represent coastal polynya sites, from left to right: Cape Darnley/Mackenzie, Barrier, Shackleton, Vincennes Bay, Dalton, and Dibble (**a**). For each 5 degree longitude bin, monthly ERA-Interim 10 m meridional winds anomalies were averaged within the minimum and maximum latitude band of average day of advance from 2004 to 2014. The correlation values from Spearman correlation between sea ice advance anomalies and averaged 10 m wind anomalies meridional component for each 5° bin of longitude are represented by the blue line; the significance of the negative correlation is represented by the dotted red line (**b**). For panel (**b**), the two dotted black lines delineate regions of interest discussed in the text. For illustration purposes, autumn correlation for sea ice concentration (March-May) is not represented. Map in panel (**a**) was made using MATLAB software (version 8.5.0.197613 (R2015a), URL http://fr.mathworks.com/).

and survival rates [Siegel and Loeb, 1995, Quetin and Ross, 2009](Figure 6b). In turn, krill and/or non-euphausiid macrozooplankton and micronekton feeding under winter sea ice [Marschall, 1988, Flores et al., 2012b, David et al., 2016] may supply the under-ice ecosystem up through to mesopelagic areas by transferring the energy to the pelagic food web (see schematic in Figure 6c) [Eicken, 1992, Reid and Croxall, 2001, Brierley and Thomas, 2002, Fraser and Hofmann, 2003, Tynan et al., 2010].

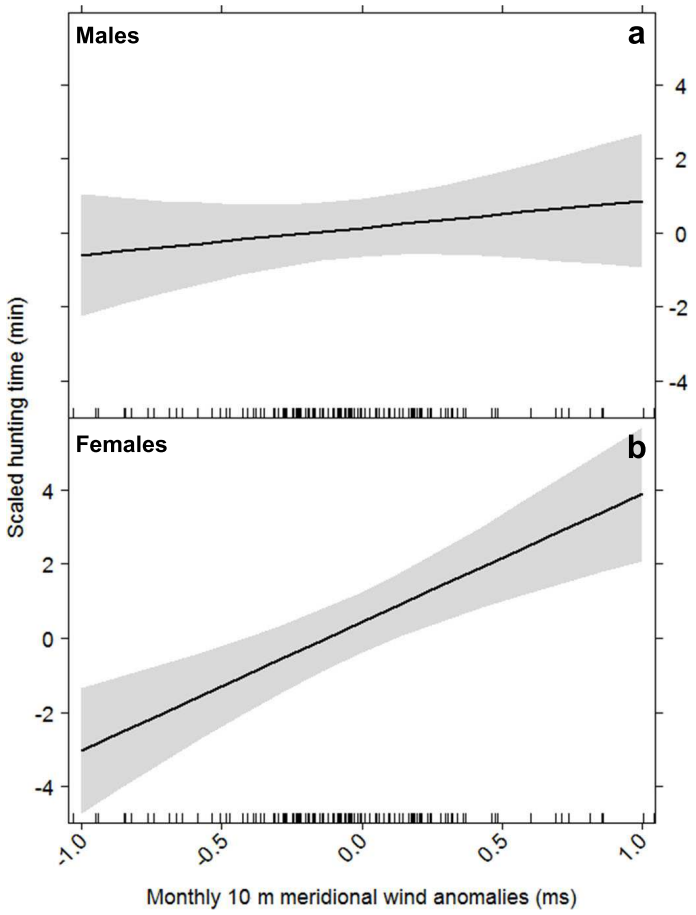


Figure IV.5: Relationships between foraging activity and meridional near-surface wind anomalies for (**a**) males and (**b**) females. Linear mixed effect models (LMMs) were used to quantify the links between foraging activity of males and females and monthly ERA-Interim 10 m meridional wind anomalies within the sea ice zone, from March to August for females and March to October for males. For each graph, the thick lines represent the predictive values from the population and the grey shaded envelopes represent the boundaries of the variation between the predicted values per individual.

Female SESs demonstrate a more than 40% increase in their hunting times when foraging in years of earlier sea ice advance. This result is in contrast to a recent study which found that earlier sea ice advance in the western Ross Sea region had a negative influence on the number of breeding seals from Macquarie Island, with a lag of 3 years [van den Hoff et al., 2014]. They suggested earlier sea ice advance would prevent seals from accessing profitable prey patch areas close to the continental shelf or within the pack ice. These contrasting results in two different regions of Antarctica highlight the difficulty associated with simply extrapolating results from one region to another, and also underline the complex linkages between seal foraging performance and sea ice characteristics. Earlier advance of sea ice may have either a positive or negative influence on foraging depending on the current state of the environment. The increasing duration of the ice season has been particularly marked in the western Ross Sea sector over the past three

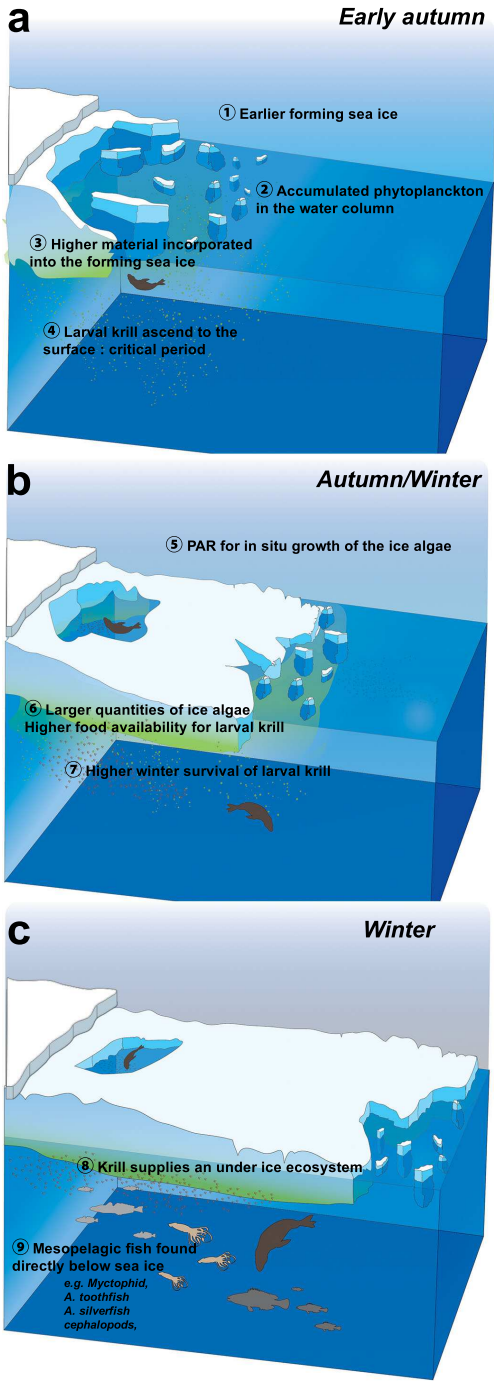


Figure IV.6: Schematic illustration of mechanisms underlying relationships between earlier sea ice advance and increased seal foraging activity. Conceptual model developed by Refs. [Siegel and Loeb, 1995, Quetin and Ross, 2009]. A critical period is when sea ice advances in autumn at a time and location where larval krill ascend to surface waters, requiring food and refuge. The earlier the sea ice formation, the greater the amount of phytoplankton incorporated from the water column into the forming ice (**a**). The greater the amount if photosynthetically available radiation (PAR) for growth of the ice algae, the higher the food availability for krill, leading to higher survival rates in juvenile krill (**b**). In turn, krill supplies an under-ice ecosystem that favours SESs in winter. For example some mesopelagic organisms usually inhabiting deep water are found directly below sea ice in the pack ice areas (**c**) [Lancraft et al., 1991, Kaufmann et al., 1995, Fuiman et al., 2002, Tynan et al., 2010]. The illustration was made by Indi Hodgson-Johnston from Adobe Stock.

decades [Stammerjohn et al., 2012], to the point where the benefit of having a more developed ecosystem readily available earlier in the season could have been negated by the increasing constraints for air-breathing predators associated with higher concentrations of sea ice cover. In contrast, in the East Antarctic sector studied here, the inter-annual sea ice duration anomalies are subtler and generally less pronounced [Massom et al., 2013], and an earlier start to the ice season appears to benefit female SESs. This situation could change, however, if season length were to considerably increase. While we found little evidence linking female foraging activity and sea ice concentration anomalies when sea ice seasonality was removed, we did find that female foraging activity increased in more concentrated sea ice, consistent with previous results III.

The linkages between sea ice and animal foraging activity are complex and dependent upon the regional setting and the spatio-temporal variability of the sea ice cover [Jenouvrier et al., 2012, Barbraud et al., 2012]. Earlier sea ice advance or increased sea ice concentration might be profitable only if SESs are able to access/locate profitable prey patches within sea ice. The Indian Ocean sector (20 – 90°E) is a region where many open ocean low concentration features occur in the ice pack associated with mesoscale eddies [Wakatsuchi et al., 1994]. Also, the western Pacific Ocean sector (90° - 160°E) is the least sea ice covered sector [Zwally et al., 2002] with generally divergent ice pack motion, dominated by leads and thin ice with a relatively large number of coastal polynyas [Tamura and Ohshima, 2011]. Thus, this regional variability in sea ice across East Antarctica might allow predators to forage within sea ice covered areas. By contrast, high sea ice coverage and persistence such as in the Western Ross sea sector might impede access to the rich under-ice ecosystems within pack ice or in polynya areas [van den Hoff et al., 2014].

In contrast to females, male hunting times increased in years with lowest sea ice concentration, and the timing of sea ice advance had a weak effect on their foraging activity. In previous studies, we showed that males remain deeper in the sea-ice zone and are able to forage on the Antarctic shelf and slope front region probably due to the presence of recurrent and persistent coastal polynyas and leads [Labrousse et al., 2015] and chapter III. Antarctic coastal polynyas, often harbouring the highest phytoplankton biomass on the relatively productive continental shelf [Arrigo and van Dijken, 2003], are sites of concentrated biological activity with rich ecosystems. As a result they support large populations of mammals that can breathe and feed throughout the ice season [Karnovsky et al., 2007]. More work is necessary to investigate the nature and drivers of inter-annual variability/change in key coastal polynyas, and their relationship with wind strength and direction [Massom, 2003], fast ice distribution [Massom et al., 1998] and sea ice seasonality. One possible caveat is that satellite passive microwave retrieval of sea ice concentration in polynyas can be inaccurate due to the presence of extensive thin ice and coastal contamination [Kwok et al., 2007]. This could compromise the accurate computation of the day of sea ice advance in polynya regions - to possibly explain why the timing of sea ice advance has an apparent significant but weak and counterintuitive effect on male foraging behaviour.

Both wind-driven dynamics and thermodynamic processes have played an important role in determining the regional complexity and variability of sea ice changes since 1979 [Holland and Kwok, 2012]. The strength of near-surface meridional winds increased female hunting times through earlier sea ice advance and increased sea ice concentrations outside polynyas and the biotic processes described above. No clear relationship was observed for males probably due to the complex influence of near-surface meridional wind anomalies on polynyas or open water areas close to the coast. Perhaps, once males are positioned in polynyas, wind-driven sea ice production and polynya size changes may not affect the prey availability or male foraging activity during the remainder of the winter season. These results compliment several studies emphasizing the complexity of wind-driven sea ice changes and its contrasting effects on Antarctic ecosystems. For example, winds (depending on strength and direction) can greatly affect higher-predator sea ice habitat by inducing: (i) ice convergence and compaction events [Massom and Stammerjohn, 2010, Massom et al., 2008] leading to thicker ice and greater constraints for air breathing predators such as seals and whales [Massom et al., 2006, Nicol et al., 2008]; (ii) loss of ice in other sectors, and loss of krill with negative effects on for example the krill-feeding crabeater seal (*Lobodon carcinophagus*) [Siniff et al., 2008]; and (iii) spatio-temporal variability in fast ice distribution [Fraser et al., 2012], with contrasting effects e.g., on emperor penguins i.e., positive associated with larger polynyas or lower fast ice extent but also negative resulting from changes in fast ice persistence for breeding [Massom et al., 2009].

We observed in the present study that both local anomalies of sea ice concentration and advance are (at least partly) controlled by local near-surface winds. Reference [Bintanja et al., 2014] has predicted a slight weakening of coastal surface winds during the 21^{st} century, becoming less katabatic in nature which may effect the "sea icescape", prey availability and access for air breathing predators through the persistence and timing of polynya opening, sea ice expansion and thinning. Although highly speculative, it is interesting to put these predicted changes in the context of the results presented in this study. Weakening of katabatic winds probably inducing later sea ice advance and decreased sea ice concentration might affect predator foraging success since Antarctic ecosystems are not only adapted to sea ice presence but also to its seasonal rhythms and properties [Massom and Stammerjohn, 2010]. However, it is important to consider that seals may have the behavioural flexibility or adaptive capacity to cope with long term changes [Younger et al., 2016].

Our study describes for the first time the significant combined effects of the interannual variability of near-surface winds as they affect sea ice coverage on the foraging activity of a predator (based upon an 11-year time series). It has also proposed mechanisms by which climate forcing affects both abiotic and biotic components of the Antarctic marine ecosystem. Understanding responses to environmental change is particularly important in the case of predators, which play crucial roles in regulating ecosystems [Baum and Worm, 2009]. The spatial heterogeneity of sea ice changes in East Antarctica [Massom et al., 2013] makes this region unique for our understanding of ecological pro-

cesses taking place between top predators and sea ice changes. We have proposed mechanisms by which sea ice changes might have direct effects on top predators through trophic cascading processes. Finally, this work highlights the lack of information on ecological processes taking place in the under-ice ecosystems up to mesopelagic areas, and in winter in particular.

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Author contributions

S.L. directed the analysis of the data set used here and shared responsibility for writing the manuscript. J-B.S., A.D.F., R.M., P.R., W.H. participated in the data analysis. J-B.S., A.D.F., R.M., P.R., W.H., M.H., J-B.C. helped in the interpretation of the results. J-B.S., A.D.F., R.M., P.R., W.H., C.G., R.H., C.M., F.B., M.H., J-B.C. shared responsibility for contributing to the final version of the manuscript.

Competing financial interests

The authors declare no competing financial interests.

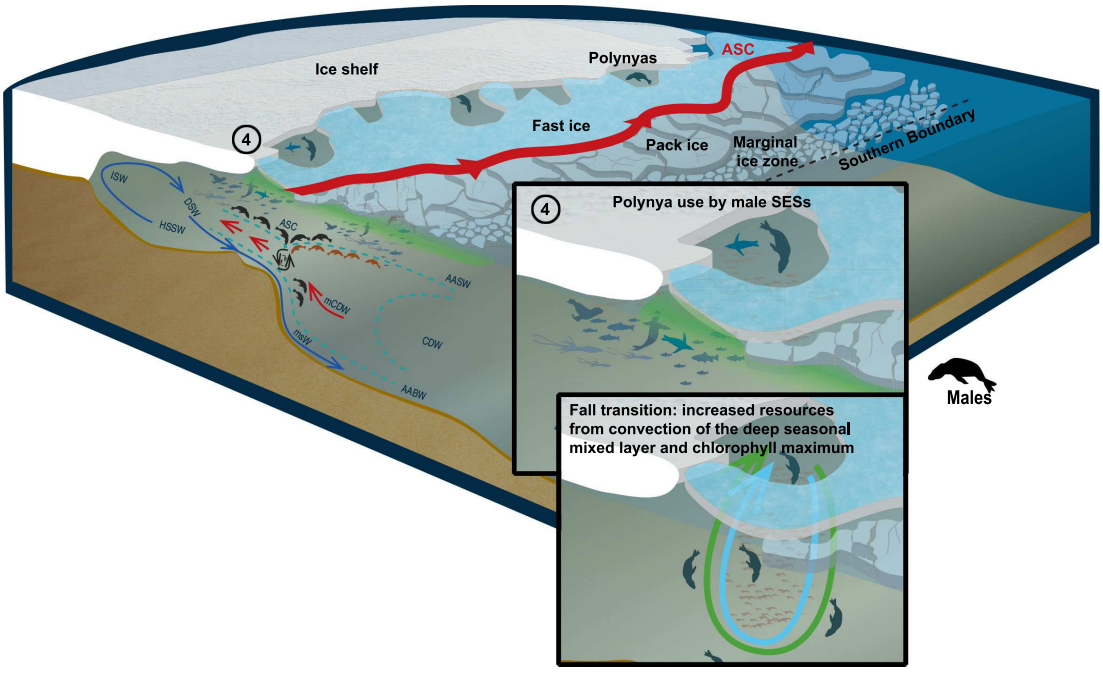
CHAPTER

V

Coastal polynyas: a winter oasis for top predators

This chapter will be submitted soon as *Coastal polynyas: a winter oasis for top predators* by S. Labrousse, T. Takeshi, A.D. Fraser, S. Bestley, J-B. Sallée, M. Sumner, G. Williams, F. Roquet, C. Guinet, R. Harcourt, C. McMahon, F. Bailleul, M.A. Hindell and J-B. Charrassin.

Schematic of the results from chapter V. Refer to the general discussion 5 for detailed caption.



Finally, I found it mysterious that males were able to remain on the shelf during the winter months in dense and persistent sea ice conditions. Moreover, male foraging activity was always associated with low patches of sea ice concentration despite individuals being in dense sea ice covered regions. The presence of recurrent and persistent open water areas, presumably harboring high biological activity, found within the dense sea ice raised my interest further. I therefore decided to end this thesis by focusing on the role coastal polynyas may play in the winter foraging behaviour of male SESs. This fourth chapter also contributes to our understanding of the role of sea ice conditions and its features in shaping prey distribution and predator foraging effort and movements in Antarctica.

Abstract

Polar marine predators depend upon an extensive set of trophic levels. Understanding their reliance to key physical and biological features is crucial to deepening our knowledge on the structure and function of polar ecosystems. Southern elephant seals (*Mirounga leonina*) represent a major consumer of Southern Ocean resources and among the different large scale foraging strategies demonstrated by the species some individuals migrate to Antarctic shelf waters. One key physical feature of Antarctic shelf waters is the presence of persistent open water areas referred to as Antarctic coastal polynyas, which offer easy access to open water within the winter sea ice cover, especially for Southern elephant seals, which are not able to maintain breathing holes. In addition, Antarctic coastal polynyas often harbor high biological productivity in spring leading to extended secondary production. The seasonal blooms persist over time, maintaining biologically rich ecosystems that may support large populations of feeding seabirds and mammals throughout the ice season. Here, we investigated the seasonal use of polynyas by male elephant seals in East Antarctica during winter. We assessed whether diving and foraging behaviour was affected by rates of sea ice formation in the polynyas and whether specific oceanographic conditions differed between polynyas and surrounding winter sea ice regions within the Antarctic shelf/slope. To do this, we studied track and diving behaviour of 23 juvenile males equipped with satellite-linked data recorders between 2004 and 2014, which undertook post-moult trips from Kerguelen Island to the Antarctic shelf. Coastal polynyas were defined using sea ice production and thin ice thickness data, calculated from passive microwave satellite data (Special Sensor Microwave Imager SSM/I). For the first time, we demonstrated that coastal polynyas in East Antarctica were true winter oasis for this mesopredator. A total of 18 males visited 9 different polynyas, spending in average 25 ± 20 % of their total recorded trip inside polynyas and up to 75%. The foraging activity was significantly higher and dives shallower inside polynyas (296 ± 159 m) compared to outside (350 ± 201 m, in the shelf, median ± standard deviation). Inside polynyas and over the shelf, seals performed both pelagic and benthic dives in similar proportion (45 ± 34 % and 55 ± 34 % respectively). Foraging activity was higher in cold Antarctic surface water inside polynyas possibly because prey are slowed down by low temperatures. Two different strategies were observed: one group (12 seals)

spent relatively short time early in the season (January - April) in post-polynyas; a second group (9 seals) remained in polynya for the whole post-moult period (February – October). The fall transition in the water column stratification (in June) was found as a key timing for the winter foraging ecology of elephant seals, corresponding to the highest foraging activity, the longest dive durations, and the deepest dives of the season inside polynyas. We hypothesized that seals may take advantage of the secondary production resulting from the deepening of the seasonal mixed-layer, entraining the remnant deep chlorophyll maximum into the surface layer and presumably stimulating an autumn bloom.

1 Introduction

Within polar ecosystems, polynya regions are thought as winter oasis harboring favorable physical and biological conditions for ecosystems, though such conditions are still loosely described. In addition, the seasonal use of polynyas and underlying mechanisms by which these regions are profitable from mid- to upper trophic levels are still poorly known. Antarctic coastal polynyas are persistent and recurrent regions of open water (no ice, thin ice, or reduced ice concentration), from tens to tens of thousands of square kilometers, which occur within the sea ice zones [Barber and Massom, 2007]. According to their mechanism of formation and maintenance, coastal polynyas have been named latent heat polynyas in contrast with offshore sensible heat polynyas. Coastal polynyas are mechanically driven and form in regions of divergent ice motion due to prevailing winds, oceanic currents, and/or dynamical barriers blocking the passage of pack ice. Such conditions promote the formation of new sea ice from the heat lost from the ocean to the atmosphere [Morales Maqueda, 2004, Tamura et al., 2016]. Surface waters associated with polynyas are often biologically productive because they are the first polar marine systems in spring to be exposed to solar radiation, either because they are not covered by sea ice or because their weak ice cover is more susceptible to early breakout in spring [Arrigo and van Dijken, 2003]. They are associated with phytoplankton blooms, which persist even after sea ice has disappeared in summer, generally maintaining the highest phytoplankton biomass on the relatively productive continental shelf [Arrigo and van Dijken, 2003]. The edges of polynyas, characterized by highly deformed sea ice, provide a favorable habitat for sea ice algae grazers [Daly and Macaulay, 1988, Marschall, 1988, Stretch et al., 1988, Schnack-schiel et al., 1994, Deibel and Daly, 2007] and enhanced vertical carbon flux in polynyas supports rich benthic communities [Grebmeier and Barry, 2007]. While enhanced primary production happens between early spring and summer, it appears to extend feeding and reproduction of zooplankton into late summer and early autumn (reviewed by Deibel and Daly [Deibel and Daly, 2007]). Therefore, Antarctic coastal polynyas are sites of concentrated biological activity with presumably rich ecosystems that may support large

populations of mammals being able to breathe and feed throughout the entire ice season [Arrigo and van Dijken, 2003, Karnovsky et al., 2007, Tremblay and Smith Jr., 2007, Arrigo et al., 2015].

Despite the numerous latent-heat polynyas in Antarctica and their potential importance for material and energy transfer within ecosystems [Karnovsky et al., 2007], our understanding of the functioning of ecosystems within polynyas is mostly based on hypothesis and is still poorly known. Several studies investigated the timing and environmental factors controlling the primary production within polynyas (e.g. [Arrigo and van Dijken, 2003, Tremblay and Smith Jr., 2007, Arrigo et al., 2015]). However, the links toward higher levels of the food web remain largely unknown. For instance, it is still not well understood if and how marine mammals and birds use polynyas both as a refuge and a foraging habitat within the winter season. The role of polynyas as a predictable open water access to food has been put forward for over-wintering or migrating species (e.g. Emperor penguins; [Kirkwood and Robertson, 1997b, Massom et al., 1998]; Adélie penguins; [Ainley, 2002, Arrigo and van Dijken, 2003]) by reducing the commuting time and energy expenditure between colony and food supply. It is also now widely accepted that spring/summer use of polynyas by upper trophic levels is associated with the seasonal primary production bloom, for example, the magnitude of primary production in polynyas was positively linked with Adélie penguin colony size [Arrigo and van Dijken, 2003] and Weddell seal probability of producing pup [Paterson et al., 2015]. However such couplings are not always clear, for example enhanced primary production in the Ross sea polynya does not appear to increase biomass of upper trophic levels [Tremblay and Smith Jr., 2007, Dugger et al., 2014]. Specific environmental conditions, such as hydrological properties, polynya size and sea ice production may be responsible of their ecological role. Moreover, determining if polynyas are still favorable for meso- to apex predators during the freezing period remains a challenge (in this paper, we abusively refer to polynyas for spring/summer season, while outside the freezing period; in spring/summer, polynyas are actually "post-polynyas"). To advance on these complex issues, it is central to better understand the underlying mechanisms explaining how the upper trophic levels benefit from polynyas (when they do).

In the present study, we investigated the use of coastal polynyas in East Antarctica by an iconic meso-predator of the Southern Ocean, the southern elephant seal (*Mirounga leonina*; SES). Circumpolar deep-diving organisms [Hindell et al., 1991a], SESs spend 80% of their time at-sea performing long migration between their breeding colonies in sub-Antarctic Islands and their foraging grounds [Hindell et al., 1991b, McConnell et al., 1992]. Key foraging habitat for SES have found to be sex-dependent [Bailleul et al., 2010a, Labrousse et al., 2015], as well as dependent on breeding subpopulation [Biuw et al., 2007, Hindell et al., 2016]. Among SESs from Kerguelen Islands, two post-moulting foraging strategies have been identified; some individuals use the Kerguelen shelf or frontal regions of the Antarctic Circumpolar Current (ACC), while others travel south within sea ice covered areas to reach the peri-Antarctic shelf [Bailleul et al., 2010a]. Despite SESs be-

ing always considered as a "non-sea ice obligate species", some individuals spent their whole post-moult foraging trip from January to October within the Antarctic region seasonally covered by sea ice [Bornemann et al., 2000, Bailleul et al., 2007a, Biuw et al., 2010, Labrousse et al., 2015, Hindell et al., 2016]. Male SESs were found to remain on the Antarctic shelf despite dense and persistent pack and fast ice, and it was previously observed and hypothesized that male SESs might use predictable and recurrent coastal polynyas or open water areas between the pack and the fast ice [Labrousse et al., 2015, Raymond et al., 2015]. Within coastal polynyas, they may take advantage of the enriched ecosystems relative to sea ice covered regions and permanent breathing access during the winter season.

We analysed male SES movements and diving behaviour collected over seven years (from 2004 to 2014) toward understanding how male SESs interact with polynya. First, (i) we assessed whether SESs used polynyas and the timing associated with this utilization (when they use them and for how long); second, (ii) we investigated how the seal diving behaviour is modified inside polynyas, and examined whether polynyas are more favourable foraging grounds than the surrounding winter sea ice covered areas in the Antarctic shelf/slope; Finally, (iii) we explored the environmental conditions that make these habitats more suitable than adjacent waters, how these conditions change over the season and, if so, how the seasonal change affects seal foraging and diving behaviour. For the first time, we demonstrated that coastal polynyas in East Antarctica are a key winter habitat for SESs from Kerguelen Islands. Unique hydrographic properties were identified and along with enhanced and extended primary and secondary production may hold the answer to the causes underpinning seal use of coastal polynyas. Two different strategies were observed among seals with implications of both post-polynyas and polynyas, suggesting different peak in prey abundance within the season. Especially, the fall transition may be a key moment in the winter foraging ecology of SESs and in the role of polynyas as winter oasis for meso-apex predators.

2 Methods

2.1 Animal handling, deployment, data collected and filtering

We used location and dive depth data from 23 post-moulting Kerguelen male SESs that were instrumented with CTD-SRDLs (Sea Mammal Research Unit, University of St Andrews) between December and February in 2004, 2008-2009 and 2011-2014 at Kerguelen Islands (49°20'S, 70°20'E) representing a total of 136,599 transmitted dives (Appendix D, DX1). These animals were chosen from a larger dataset because they visited the area south of 55°S (the spatial domain for the study), which corresponds to the maximum latitude of annual sea ice extent (in September). From the larger dataset, only one female out of 23 visited polynyas, suggesting that this is an uncommon behaviour in females, and therefore only males were studied. Details on instrumentation, seal handling and data processing for dives, ARGOS positions filtering and temperature and salinity profiles treatment are pro-

vided in Labrousse et al. [Labrousse et al., 2015]. All animals in this study were handled in accordance with the French Polar Institute (Institut Paul Emile Victor, IPEV) ethical and Polar Environment Committees guidelines. The experimental bio-logging protocol was approved by the same Committees.

2.2 Foraging activity and time spent

Foraging activity of each seal was analysed in two ways: (i) at the dive scale using the methodology developed by [Heerah et al., 2015], which estimates the time spent hunting during a dive. For each dive, the time spent in segments with a vertical velocity lower or equal to 0.4 $m.s^{-1}$ was calculated. This time was termed hunting time per dive and was used as a proxy for foraging activity; (ii) at the daily scale, prey encounter events per day (PEE) were predicted based on dive and trajectory parameters following Labrousse et al. [Labrousse et al., 2015].

Time spent within or outside polynyas, in the different cores, zones, shelf, slope and open ocean and within benthic or pelagic strategies were computed from the dive duration of the dive data except for individuals 2011-4 and 2011-9 (marked with a star in Table V.2). For these two individuals, CTD data were used instead because the dive data stopped recording at-sea in May while the CTD continued until September. For these individuals, the time spent inside and outside polynyas over the whole trip, in the different cores, zones (shelf, slope and open ocean) and within benthic or pelagic strategies was computed using the number of CTD observations in each case divided by the total number of CTD observations. For consistency between individuals, figures V.3 and V.4 were based on time spent computed from CTD casts for all individuals.

2.3 Polynya identification

Polynya determination was based on a sea ice production (SIP; expressed in $m.y^{-1}$) threshold. The estimation of SIP followed Tamura et al. [Tamura and Ohshima, 2011]. First, thin ice thickness was estimated using the Tamura et al. [Tamura et al., 2007] algorithm, using 85 and 37 GHz brightness temperature retrieved from SSM/I. Next, SIP was estimated by heat flux calculation during the freezing period (from March to October) using thin ice thickness and surface atmospheric data. The air-sea ice surface heat flux is obtained by assuming that the sum of radiative and turbulent fluxes at the ice surface is balanced by the conductive heat flux in the ice. The European Centre for Medium-Range Weather Forecasts Re-Analysis data (ERA-40: 1992–2001, ERA-interim: 1992–2013) and the National Centers for Environmental Prediction/Department of Energy Re-Analysis data (NCEP2: 1992–2013) were used for this calculation. The calculation was performed twice a day over the entire Southern Ocean on the SSM/I Equal Area Scalable Earth-Grid (12.5 km × 12.5 km) from 1992 to 2014.

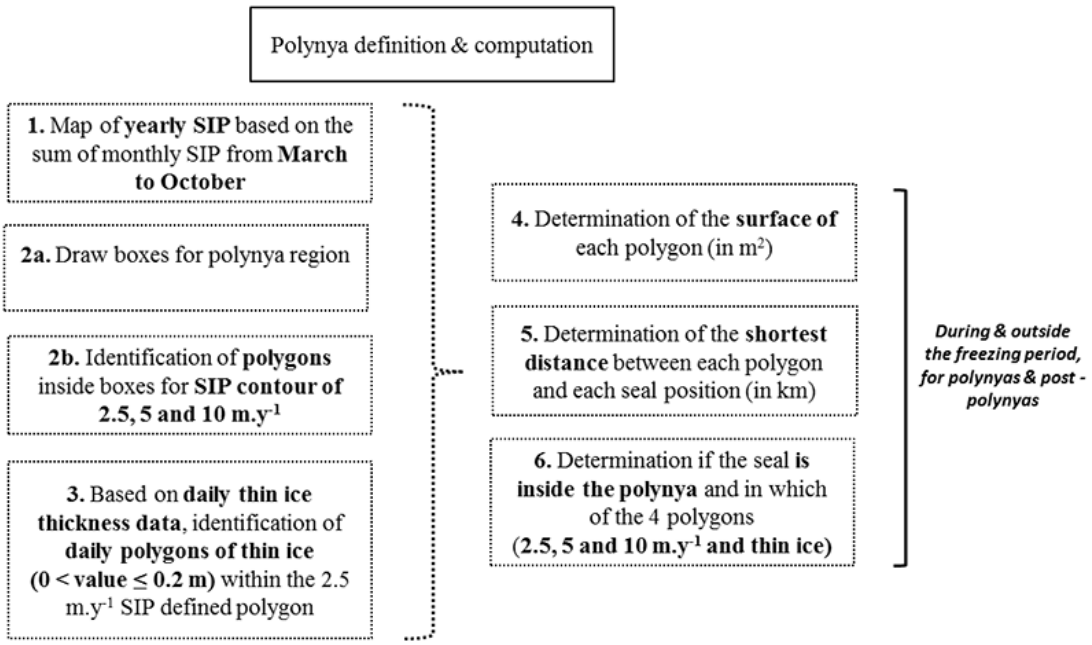


Figure V.1: Schematic representing the different steps for polynya definition and the calculation of SESs use of polynyas.

The determination of polynyas in the study region followed the steps presented in Figure V.1. We first determined the yearly SIP for each year, SIP_{year}, by summing monthly SIP during the freezing period (from March to October; step 1, Figure V.1; Panel a, Figure V.2). Then, we defined boxes around known polynya regions based on literature information [Massom et al., 1998, Arrigo and van Dijken, 2003, Arrigo et al., 2015, Nihashi and Ohshima, 2015], and within these boxes, we draw three polygons to define polynya regions based on the contour of SIP_{year} corresponding to 2.5 $m.y^{-1}$ (green contour), 5 $m.y^{-1}$ (yellow contour) and 10 $m.y^{-1}$ (red contour) (step 2a and 2b, Figure V.1; Panel b and c, Figure V.2). For contouring SIP_{year}, we used the package *raster* (from R Development Core Team) with the function *rasterToContour* and the package *rgeos* with the function *gPolygonize*. Then, based on daily estimates of thin ice thickness, within the larger polygon defining the contour of 2.5 $m.y^{-1}$ of SIP_{year}, we contoured, for each polynya, a polygon of thin ice (characterized by a thickness from 0 to 0.2 m, blue contour; step 3, Figure V.1; Panel d, Figure V.2). The three step procedure for defining polynyas is illustrated by two yearly maps of SIP for 2004, where boxes and contours are drawn, and one daily map of thin ice thickness where SIP and thin ice contours are drawn (see Figure V.2). A total of 14 polynyas were identified and named based on Massom et al. [Massom et al., 1998] and Arrigo and van Dijken [Arrigo and van Dijken, 2003]: 1. Lützoh-Holm Bay, 2. Cape Borle, 3. Cape Darnely, 4. Mackenzie, 5. Barrier, 6. West Ice Shelf, 7. Shackleton, 8. Bowman Island, 9. Vincennes Bay, 10. Cape Poinsett, 11. Dalton, 12. Paulding Bay, 13. Dibble, 14. Mertz.

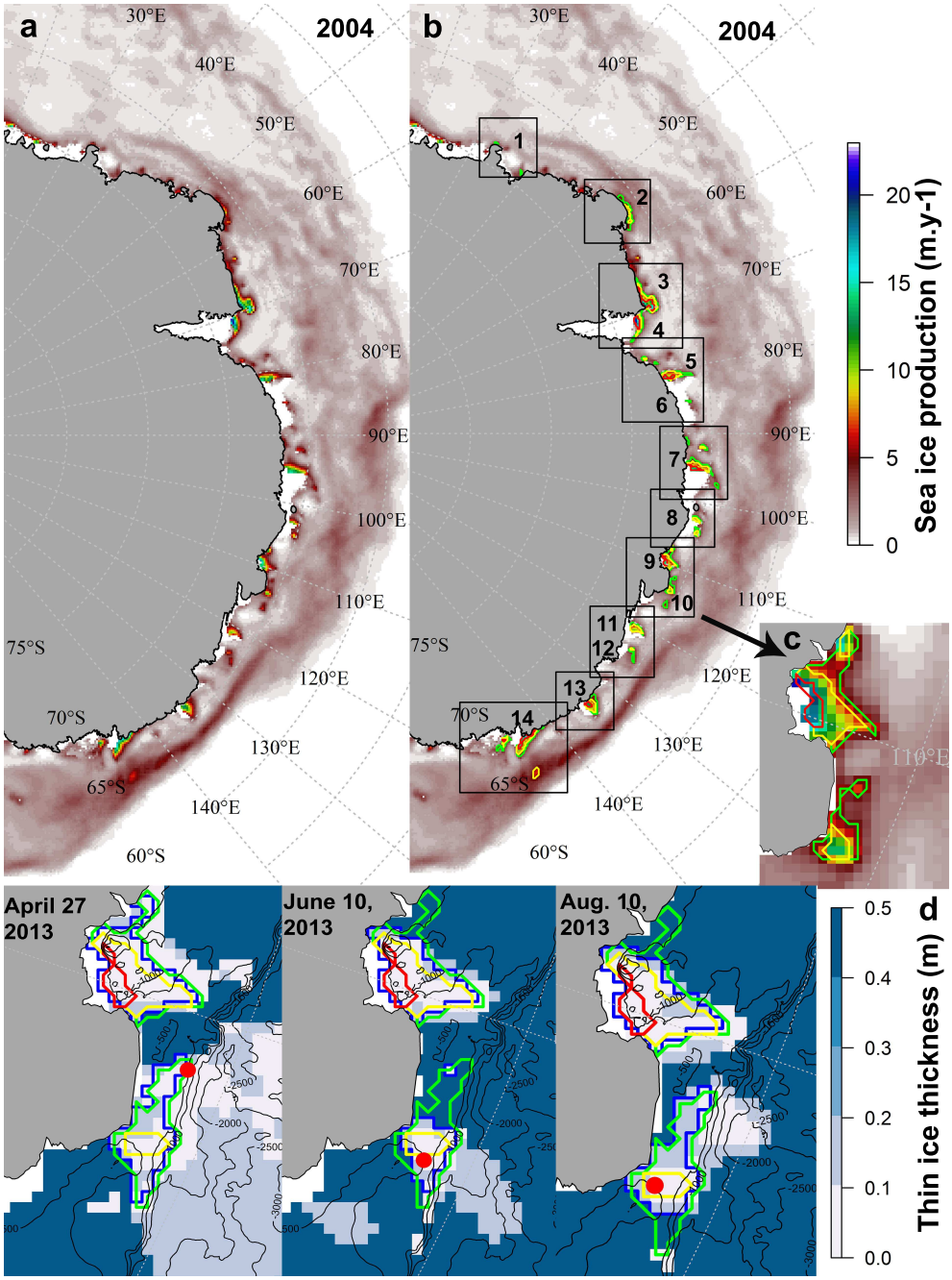


Figure V.2: Illustration of the polynya definition based on SIP and thin ice thickness. Example of yearly SIP ($m.y^{-1}$) map obtained from the sum of monthly SIP during the freezing period from March to October in 2004 (**a**). Same as (**a**) with boxes superimposed defining some polynya areas based on literature, within which polynya definition polygons were computed based on threshold of SIP of 2.5 $m.y^{-1}$ (green contour), 5 $m.y^{-1}$ (yellow contour) and 10 $m.y^{-1}$ (red contour) (**b**). A total of 14 polynyas were identified: 1. Lützoh-Holm Bay, 2. Cape Borle, 3. Cape Darnely, 4. Mackenzie, 5. Barrier, 6. West Ice Shelf, 7. Shackleton, 8. Bowman Island, 9. Vincennes Bay, 10. Cape Poinsett, 11. Dalton, 12. Paulding Bay, 13. Dibble, 14. Mertz. The insert is a zoom of polynyas 9 and 10 to highlight the different contours (**c**). Examples of map of thin ice thickness data for three days in 2013 where SIP polynya definition (i.e. 2.5 $m.y^{-1}$ (green contour), 5 $m.y^{-1}$ (yellow contour) and 10 $m.y^{-1}$ (red contour)) and bottom topography are superimposed (**d**). Within the green polygon (i.e. the larger polynya definition based on SIP), polygons of thin ice were daily drawn for thickness comprised between 0 and 0.2 m (blue contour). The red dot corresponds of one the seal position for this given day.

As such, for each of the 14 polynyas, we define a yearly position of the polynya, based on three thresholds corresponding to three yearly-mean "cores" of the polynya, from less to more active: SIP_{year} equal to 2.5 $m.y^{-1}$; 5 $m.y^{-1}$; or 10 $m.y^{-1}$. In addition, we define the “daily core” region of the polynya, corresponding to the region with the thinnest thin ice within the yearly polynya core: thin ice thickness less than 0.2 m. By determining the "daily core" of the polynya from the thin ice contours, we characterized the variability of the distribution of thin ice from one day to another inside the polynya region defined with a yearly SIP_{year}. Note that these "daily core" were derived for each day of the seals' track, including periods outside the freezing period. While, a polynya is often defined as an area of open water or reduced sea ice cover located in waters that would be expected to be ice covered (i.e. is considered as a wintertime phenomena), in this study, we abusively refer to as polynya in spring/summer, as surface waters after the retreat of sea-ice, within a polynya sector, are often more biologically productive than adjacent waters [Arrigo and van Dijken, 2003].

The area of each polygon (expressed in squared meter) was computed using the package *rgeos* with the function *gArea* (step 4, Figure V.1). The shortest distance between each seal position and each polygon contour was computed using the package *rgeos* and the function *spDistsN* (step 5, Figure V.1). Finally, we also determined if the seal was inside of each polygon using the package *rgeos* and the function *gContains* (step 6, Figure V.1).

2.4 In situ salinity/temperature profiles and water-mass definition

Among the 23 male SESs, 21 had usable CTD (Conductivity–Temperature–Depth) profiles for a total of 8568 profiles (Appendix D, Table DX1). All tags were initially calibrated at the laboratory and a part of them were also tested at sea against a ship based CTD before deployment. All tags were then post-calibrated using standardized procedures described in Roquet et al. [Roquet et al., 2011, Roquet et al., 2014]. The minimum accuracies of post processed data were estimated to be ± 0.03°C in temperature and ± 0.05 psu, increasing to ± 0.01°C and ± 0.02 psu in the best cases [Roquet et al., 2014].

To obtain continuous temperature and salinity vertical profiles, a linear interpolation every 5 m was applied while the average depth difference between points of each profile among all individuals were 35 ± 45 m (mean ± standard deviation). CTD positions were corrected by interpolating filtered locations from state-space models along the track based on the CTD date and time.

For each CTD profile, we identified the water masses used when the seals were foraging at the bottom phase, as this is where most of the foraging activity is expected to occur [Guinet et al., 2014]. The start of the bottom phase was defined as 80% of the maximal depth of the CTD profile. We also identified the water mass at the maximal depth of each CTD profile.

To associate temperature and salinity profiles (average of 2.8 ± 1 (SD) profiles per day, n = 21) with foraging activity and dive parameters (e.g. dive duration) determined from dive data (average of 41 ± 19 (SD) dives per day, n = 23), each CTD profile was associated with

Table V.1: Definition criterion of water masses determined from CTD-SRDLs temperature, salinity, pressure collected by the 21 post-moulting Kerguelen male SESs at the bottom phase of dives from 2004 to 2014 along tracks from 55°S to the Antarctic continent and from 30 to 150°E.

Acronym	Type of water mass	Neutral density γ_n (kg.m^{-3})	Potential Temperature θ (°C)	Depth D (m)	Zone
AASW	Antarctic Surface Water	$\gamma_n \leq 28.0$			
CDW	Circumpolar Deep Water	$28.0 < \gamma_n < 28.27$	$\theta > 1.5$		
mCDW	modified Circumpolar Deep Water	$28.0 < \gamma_n < 28.27$	$-1.8 < \theta < 1.5$		
mSW-north	modified Shelf Water (north of the shelf break)	$\gamma_n \geq 28.27$		D < 2500 m	
mSW-south	modified Shelf Water (south of the shelf break)	$\gamma_n \geq 28.27$	$\theta > -1.8$		Antarctic Shelf
AABW	Antarctic Bottom Water	$\gamma_n \geq 28.27$		D ≥ 2500 m	
ISW	Ice Shelf Water		$\theta \leq -1.95$		
DSW	Dense Shelf Water	$\gamma_n \geq 28.27$	$-1.95 < \theta < -1.8$		
LSSW	Low Salinity Shelf Water (south of the shelf break)	$28.0 < \gamma_n < 28.27$	$-1.95 < \theta < -1.8$		Antarctic Shelf

the closest dive in time and depth collected by the same individual following the different steps: (i) for each CTD profile, only dives with a maximal depth shallower or equal to the maximal depth of the CTD profile were retained; (ii) from this first selection, only dives within the CTD time window of ± 6 hours were retained; (iii) from this second selection, the dive from which the maximal depth was the closest to the CTD profile maximal depth was retained; (iv) if more than one dive were retained from the previous selection, the closest in time was selected.

The stratification from the surface to the maximal depth of the dive (expressed as the frequency of Brunt-Väisälä, $N^2 = g / \rho_0 \cdot \delta\sigma_0 / \delta_z$) was calculated by dividing the difference between the surface-referenced potential density (σ_0) at the surface and at the bottom (expressed in kg.m^{-3}) by the maximal depth (z) of the dive (expressed in meters), the overall divided by ρ_0 = 1000 kg.m^{-3} and multiplied by g, the gravitational acceleration of the Earth ($g \sim 9.81$ m.s^{-2}).

Water masses sampled during the transit of seals along their trip from 55°S to the Antarctic continent were then determined from their temperature, salinity and neutral density γ_n [Jackett and McDougall, 1997]. We distinguished between eight water masses: (1) Antarctic Surface Water (AASW); (2 and 3) modified and Circumpolar Deep Water (CDW, mCDW); (4) modified Shelf Water, north and south of the shelf break (mSW); (5) Antarctic Bottom Water (AABW); (6) Ice Shelf Water (ISW); (7) Dense shelf water (DSW); (8) Low Salinity Shelf Water (LSSW). Criteria to define these water masses were adapted from [Labrousse et al., 2015, Hindell et al., 2016] following the basic water mass definitions of [Orsi, 1995, Whitworth et al., 1998, Orsi and Wiederwohl, 2009, Bindoff et al., 2000, Meijers et al., 2010, Lacarra et al., 2011, Williams et al., 2016]. Water masses definition is summarized in Table V.1.

2.5 Statistical analysis

In an attempt to describe the influence of (i) polynyas, (ii) oceanographic conditions within polynyas and (iii) the seasonality within polynyas on seal foraging activity, diving depths and dive duration, a total of 10 linear mixed effects models (LMMs) were fitted with the R package *nlme* (from R Development Core Team, function *lme*) using restricted maximum likelihood. The 10 different models tested the significance of: 1 and 2) the difference in hunting times and maximal depths inside and outside polynyas; 3 and 4) the difference in hunting times and maximal depths in the 3 different yearly cores and outside polynyas; 5 and 6) the difference in hunting times in the different water masses sampled at the maximum depth of the CTD casts within the Antarctic shelf inside and outside polynyas; 7) the difference in hunting times in the different water masses sampled at the maximum depth of the CTD casts within the Antarctic slope combining both inside and outside polynyas, as the number of observations inside polynyas on the slope were too small to apply one single model in each case; finally 8,9 and 10) the difference in hunting times, maximal depths and dive duration inside polynyas/post-polynyas from January to October. Models were based on CTD casts associated with dive characteristics as detailed previously, on a total of 21 males.

For each model, the response variable was centred and scaled for each seal prior to analysis to correct for non-Gaussian distribution. Outliers in the variables were checked. We first determined the optimal structure by assessing if individual seals as a random intercept term contributed to the model fit. The final model was then fitted using restricted maximum likelihood (REML). Model validation was checked by plotting Pearson residuals against fitted values, and against the explanatory variable, to verify homogeneity and normality of residuals [Zuur et al., 2010].

3 Results

3.1 Polynya habitat use

Over the 23 male SES foraging trips obtained from 2004 to 2014, 18 seals visited polynya areas from January to November (Figure V.3). A total of 9 different polynyas were visited.

The different metrics describing the use of polynyas by each seal are given in Table V.2. A high individual variability is observed in terms of polynya use: seals spent from 4 to 75% of their total trip inside polynyas, rising to 5 to 86% when in the slope/shelf region. When inside polynyas, they spent more time on the shelf compared to the slope region (i.e. an average of 92 ± 16% of time on the shelf versus 8 ± 16% on the slope) and spent about 47 ± 26% in thin ice (0 to 0.2 m). Based on SIP, seals inside polynyas spent on average 60 ± 29% of their time in the core 1, 32 ± 25% in the core 2 and 8 ± 14% in the core 3. They dived benthically 54 ± 34% and pelagically 46 ± 34% of their time in polynyas. Interestingly, inside polynya over the shelf, seals performed both pelagic and benthic dives (i.e. 45 ± 34%

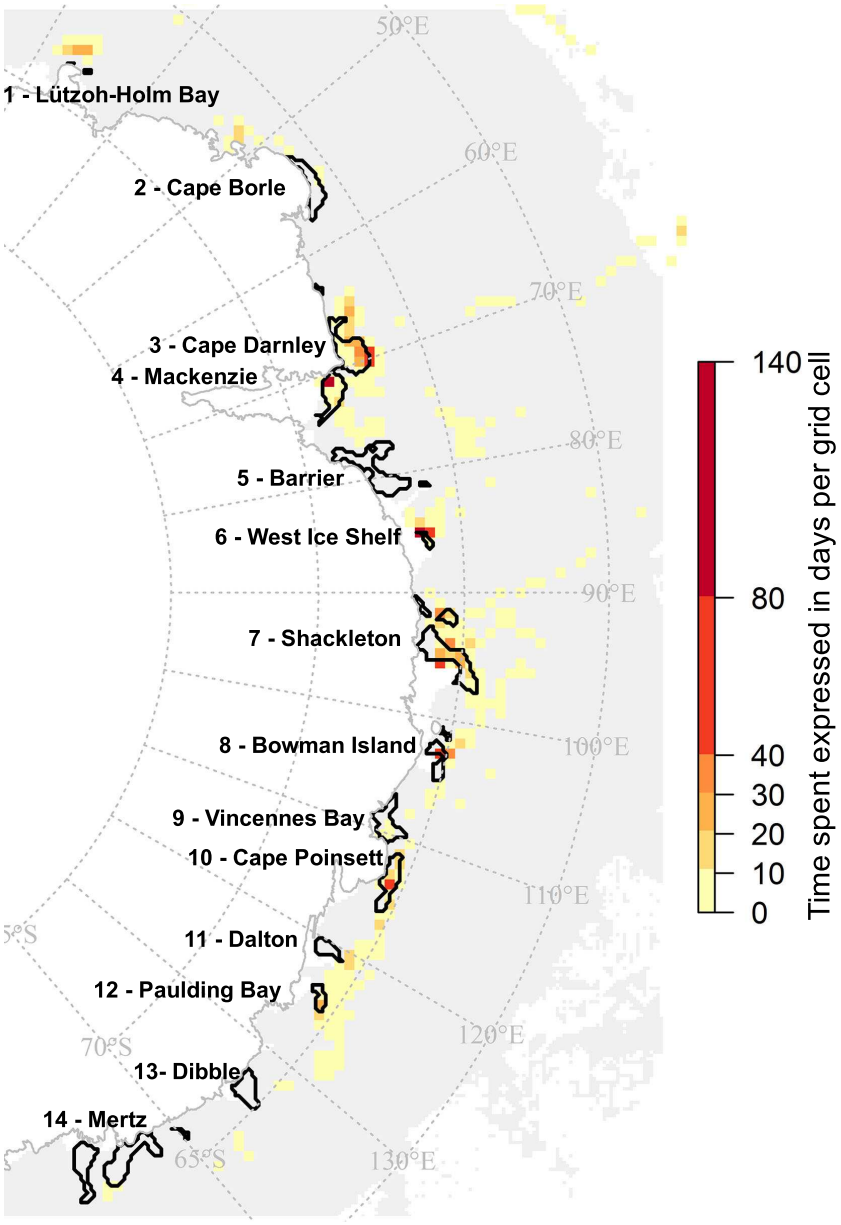


Figure V.3: Polynya use by the 21 post-moult Kerguelen male SESs from 2004 to 2014 CTD casts. A total of 23 SESs were studied however, CTD data were not available for the individual 2004-1 and 2008-1 (leading to a number of 21 SESs). Average time spent in polynyas across all individual seals per grid cell (37.5 × 37.5 km) (expressed in days) was computed using the date time of CTD casts from 2004 to 2014.

of pelagic dives and 55 ± 34% of benthic dives); similarly, both benthic and pelagic dives occurred while inside polynya over the slope (i.e. 51 ± 31% of pelagic dives and 49 ± 31% of benthic dives).

3.2 Seasonality in polynya use

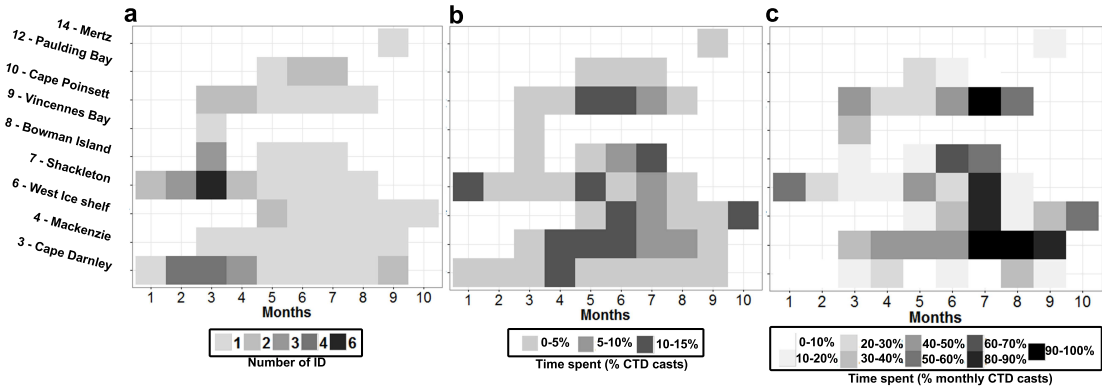


Figure V.4: Seasonality of polynya use by the 17 post-moult Kerguelen male SESs from 2004 to 2014 CTD casts. A total of 18 individuals visited polynyas however, CTD data were not available for the individual 2008-1. Panel (**a**) represents the number of individuals per month and per polynyas, panel (**b**) the time spent per polynya in a given month averaged across all seals, and panel (**c**) the time spent per polynya and per month compared to the whole trip averaged across all seals.

We expressed the seasonality of polynya use with three metrics, giving a sense of which East Antarctic polynya is used by the seals, when and for how long (Figure V.4): (i) the number of individuals inside polynyas for each month (Figure V.4a); (ii) the percentage of time spent in a given polynyas each month compared to the whole trip across all seals (the time spent in a given month was computed per individual and then averaged across all seals; Figure V.4b); and (iii) the percentage of time spent in a given polynya each month across all seals (this was also computed per seal and then averaged across all seals; Figure V.4c). Two different strategies were observed regarding the seasonal use of polynyas: one group (9 seals) spent relatively short time early in the season (January - April) in post-polynyas; in contrast, a second group (9 seals) remained in polynya for the whole post-moult period (February – October). Seals spent a larger proportion of their time in polynyas (given their monthly time and their total trip time) from April to October (Figure V.4b, c), which correspond to autumn and winter seasons. Five different polynyas were mostly used by seals, which were visited by at least two individuals during the season and where the seals spent 10-15% of their total time, namely: Cape Darnley (3), West Ice Shelf (6), Shackleton (7), Bowman Island (8), and Cape Poinsett (10).

Table V.2: General information of the 18 post-moulting Kerguelen male SESs that visited polynyas from January to November 2004 to 2014 including year, weight, time spent in polynyas (INP), the number of enter and exit in/out the polynyas, time spent in polynyas when the seal is on shelf and slope region, and information on the behaviour inside the polynyas: time spent on the shelf, time spent on the slope, time spent in thin ice, time spent in the core 1 (2.5 $m.y^{-1}$ of SIP), time spent in the core 2 (5 $m.y^{-1}$ of SIP), time spent in the core 3 (10 $m.y^{-1}$ of SIP), benthic dives, pelagic dives, pelagic dives on slope, pelagic dives on shelf, benthic dives on slope, benthic dives on shelf. Average are expressed ś SE. Statistics are computed from the dive data except for individuals 2011-4 and 2011-9 (marked with a star) where CTD data were used instead because the dive data stopped recording at-sea in May while the CTD continued until September. Individuals underlined in bold italics are individuals for which the tag did not stopped before they returned to the colony.

ID	Year	Weight (kg)	Time spent INP over the whole trip (%)	Number of enter/exits INP	Time spent INP when on shelf, slope (%)	Time spent on the shelf INP (%)	Time spent on the slope INP (%)	Time spent in thin ice (0-0.2 m) INP (%)	Time spent in core 1 (2.5 $m.y^{-1}$ of SIP) INP (%)	Time spent in core 2 (5 $m.y^{-1}$ of SIP) INP (%)	Time spent in core 3 (10 $m.y^{-1}$ of SIP) INP (%)	Benthic dives INP (%)	Pelagic dives INP (%)	Pelagic dives INP on the slope (%)	Pelagic dives INP on the shelf (%)	Benthic dives INP on the slope (%)	Benthic dives INP on the shelf (%)
2004_2	2004	385.5	21	125	25	45	55	23	94	6	0	29	71	75	66	25	34
2004_5	2004	469.5	27	62	34	100	0	21	50	50	0	100	0	0	0	100	100
2004_8	2004	274	6	69	14	100	0	13	100	0	0	24	76	_	76	_	24
2008_1	2008	266	22	89	43	99	1	94	93	7	0	82	18	100	18	0	82
2011_4*	2011	800	45	40	57	100	0	47	35	21	44	68	32	_	32	_	68
2011_7	2011	452.5	15	18	19	93	7	63	33	47	20	83	18	47	15	53	85
2011_9*	2011	628.5	21	88	22	58	42	45	56	22	22	74	26	26	26	74	74
2012_1	2012	523	9	36	11	78	22	50	54	44	2	65	35	46	32	54	68
2012_2	2012	303	52	22	68	93	7	46	67	27	7	94	6	41	4	59	96
2013_2	2013	1100	55	52	76	96	4	67	25	75	0	16	84	70	84	30	16
2013_3	2013	468	2	**4**	**5**	100	0	9	79	21	0	72	28	_	28	_	72
2013_9	2013	470	12	10	30	100	0	48	77	23	0	75	25	_	25	_	75
2013_11	2013	556	**75**	114	**86**	100	0	67	9	85	5	79	21	_	21	_	79
2013_13	2013	600	**4**	8	6	100	0	78	91	9	0	66	34	_	34	_	66
2013_14	2013	300	36	**214**	42	100	0	14	100	0	0	53	47	_	47	_	53
2014_7	2014	405	**4**	**4**	6	100	0	78	14	46	40	0	100	_	100	_	0
2014_9	2014	700	22	26	35	100	0	12	64	31	5	0	100	_	100	_	0
2014_10	2014	700	26	54	62	100	0	62	47	54	0	0	100	_	100	_	0
Average ± SE		**522 ± 212**	**25 ± 20**		**36 ± 25**	**92 ± 16**	**8 ± 16**	**47 ± 26**	**60 ± 29**	**32 ± 25**	**8 ± 14**	**54 ± 34**	**46 ± 34**	**51 ± 31**	**45 ± 34**	**49 ± 31**	**55 ± 34**

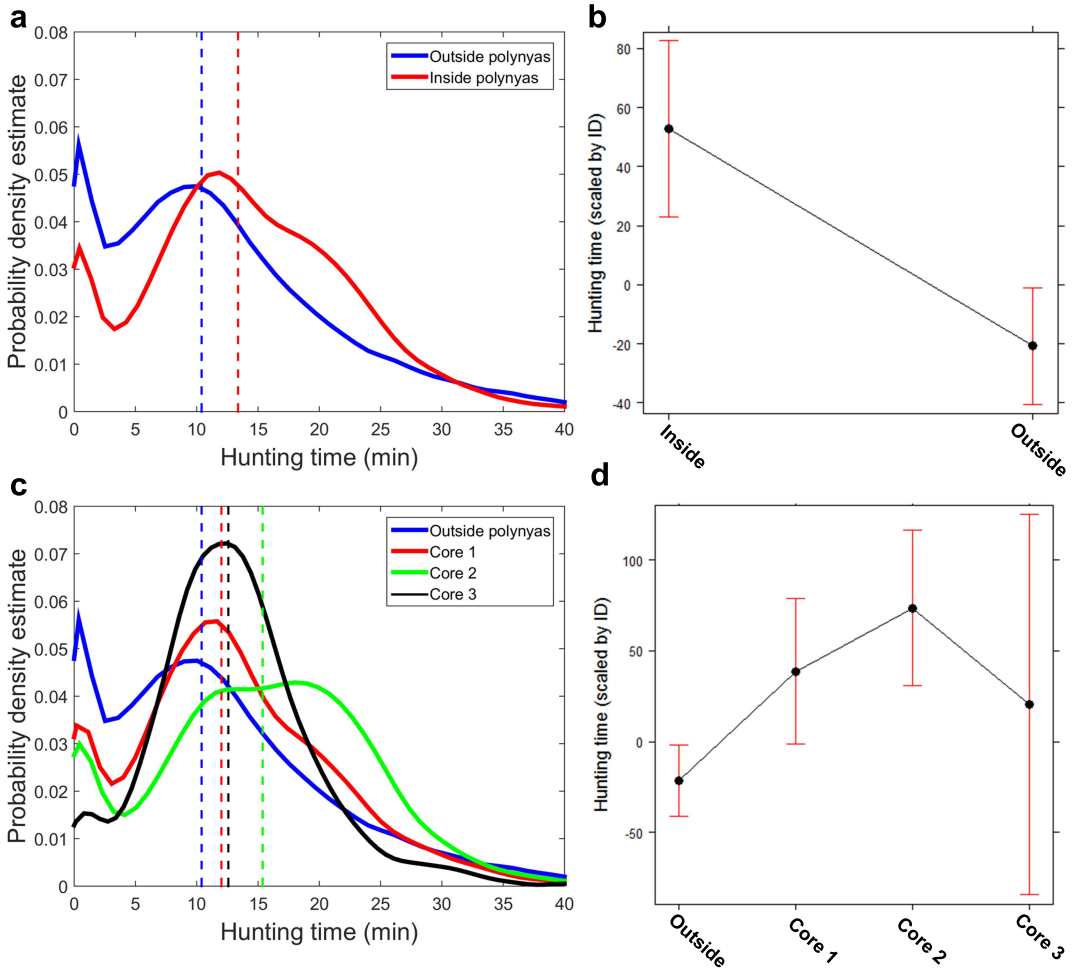


Figure V.5: Change in foraging activity (expressed by the hunting time) inside and outside polynyas and within the different cores of the polynya. The probability density estimate (PDE) inside and outside polynyas is represented in panel (**a**) and outside, in the core 1, 2 and 3 in the panel (**c**). Dashed lines represent the median of hunting time (expressed in minutes). Relationships from the two LMMs between hunting time and the position of the seal inside versus outside and the position of the seal outside and in the core 1, 2 and 3 are represented in the panel (**b**) and (**d**) respectively. The PDEs (panel **a** and **c**) were computed based on dive data (18 SESs inside polynyas and 23 SESs outside polynyas). LMMS (panel b and d) were computed based on CTD data at the bottom phase of dives (17 SESs inside polynyas and 21 SESs outside polynyas as CTD data were not available for the individual 2004-1 and 2008-1).

3.3 Change in the diving and foraging behaviour inside polynyas

Over seals' entire trips, hunting time was significantly higher inside the polynyas compared to outside polynyas (i.e. seals spent 13.4 ± 8.6 min (median ± standard deviation) hunting inside polynyas compared to 10.4 ± 9.7 min outside polynyas; Figure V.5a, b). They also hunt significantly longer in the core 1 and 2 of the polynyas (defined by SIP_{year} of 2.5 and 5 $m.y^{-1}$ respectively) compared to outside polynyas (i.e. seals spent 12.0 ± 8.5 min (median ± standard deviation) hunting in the core 1, 15.4 ± 8.9 min in the core 2 and 12.6 ± 6.6 min in the core 3; Figure V.5b, c).

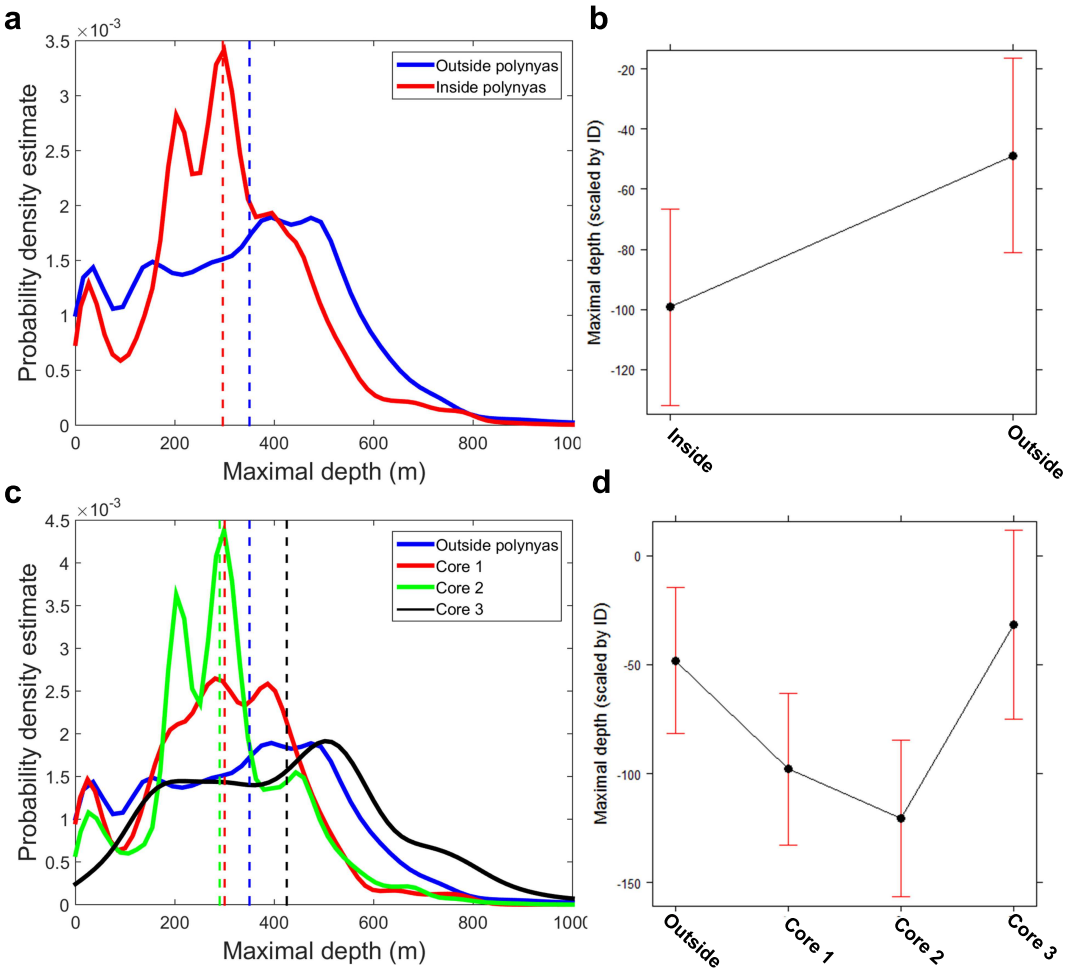


Figure V.6: Change in diving depths (expressed by the maximal depth in meters) inside and outside polynyas and within the different cores of the polynya on the Antarctic shelf region. The probability density estimate (PDE) inside and outside polynyas is represented in panel (**a**) and outside, in the core 1, 2 and 3 in the panel (**c**). Dashed lines represent the median of diving depth (expressed in meters). Relationships from the two LMMs between maximal diving depth and the position of the seal inside versus outside and the position of the seal outside and in the core 1, 2 and 3 are represented in the panel (**b**) and (**d**) respectively. The PDEs (panel **a** and **c**) were computed based on dive data (18 SESs inside polynyas on the shelf and 21 SESs outside polynyas on the shelf). LMMS (panel **b** and **d**) were computed based on CTD data at the bottom phase of dives (17 SESs inside polynyas on the shelf and 20 SESs outside polynyas on the shelf as CTD data were not available for the individual 2004-1 and 2008-1).

We also compared diving depths inside and outside polynyas but here we focused on the Antarctic shelf region where bathymetry is relatively constant. Indeed, comparing diving depths by considering both the Antarctic shelf/slope and abyssal plains north of the shelf break could be misleading because differences in diving depth could primarily reflect bathymetry variations instead of the presence of polynyas. Seals made significantly shallower dives inside the polynyas compared to outside polynyas (i.e. seals dived at 350 ± 201 m (median ± standard deviation) outside polynyas compared to 296 ± 159 m in-

side polynyas; Figure V.6a, b). They also dived significantly shallower in core 1 and 2 of the polynyas compared to outside polynyas (i.e. seals dived at 300 ± 155 m (median ± standard deviation) in core 1, 290 ± 147 m in core 2 and 425 ± 212 m in core 3; Figure V.6b, c).

Seals had shorter hunting times and dived deeper in core 3 of the polynyas (defined by SIP_{year} of 3 $m.y^{-1}$), but this was not significantly different from outside polynyas. However, dive observations in core 3 represented only 6.7% of all dives in polynyas, so the ecological importance of such dives is probably low.

Finally, no significant differences were found in dive durations inside polynyas and outside and between the different cores within the Antarctic shelf region (Appendix D, Figure DX1).

3.4 Oceanographic conditions and foraging behaviour inside polynyas

On the Antarctic shelf, seals dived in 5 different water masses, AASW, LSSW, MSW, DSW and ISW (Figure V.7a, d). However, when diving inside polynyas, they hunt significantly longer in the AASW (Figure V.7b), and qualitatively (the relationship was not statistically tested with the PEE foraging index) more PEE were predicted in this water mass (Figure V.7c). In contrast, water-masses had no particular effect on hunting time when seals were foraging outside polynyas (Figure V.7e, f).

On the Antarctic slope, seals dived in 3 different water masses, AASW, MCDW, and MSW (Figure V.8a and inset). In contrast, ISW represented only 0.1% of the water-masses sampled at the bottom of dives; DSW only 0.5%; and CDW only 0.2%; we therefore ignored ISW, DSW and CDW in the following statistical analysis of the slope region. CTD casts inside polynyas represented only 6.8% of the total CTD casts on the slope region, and was not sufficient to build one single model linking foraging activity with water masses inside polynyas on the slope region. We thus built a model combining observations inside and outside polynyas on the slope region. Although the relation was not significant, seals tended to hunt longer in the MCDW (Figure V.8b) and qualitatively the largest PEE were observed in both MCDW and MSW (Figure V.8c).

3.5 Effect of the seasonality of oceanographic conditions inside polynyas on foraging activity

Inside polynyas, diving depth, dive duration and hunting time had all significant seasonal variations with a clear maximum in June. Hunting time and dive duration regularly increased from January to June before slowly declining until October, while monthly dive depth were relatively constant until June before dropping markedly thereafter (Figure V.9a, b, c). In June, AASW was predominant at the bottom of seals' dives (Figure V.10a), and seals' hunting time was longer in AASW compared to other water-masses (Figure V.7b). AASW sampled by seals inside polynyas have their own seasonal variations, and June was associated with their seasonal minimum in salinity and neutral density, and with a plateau in the seasonal destratification (Figure V.10c, d, e). June seems therefore has a distinctive months

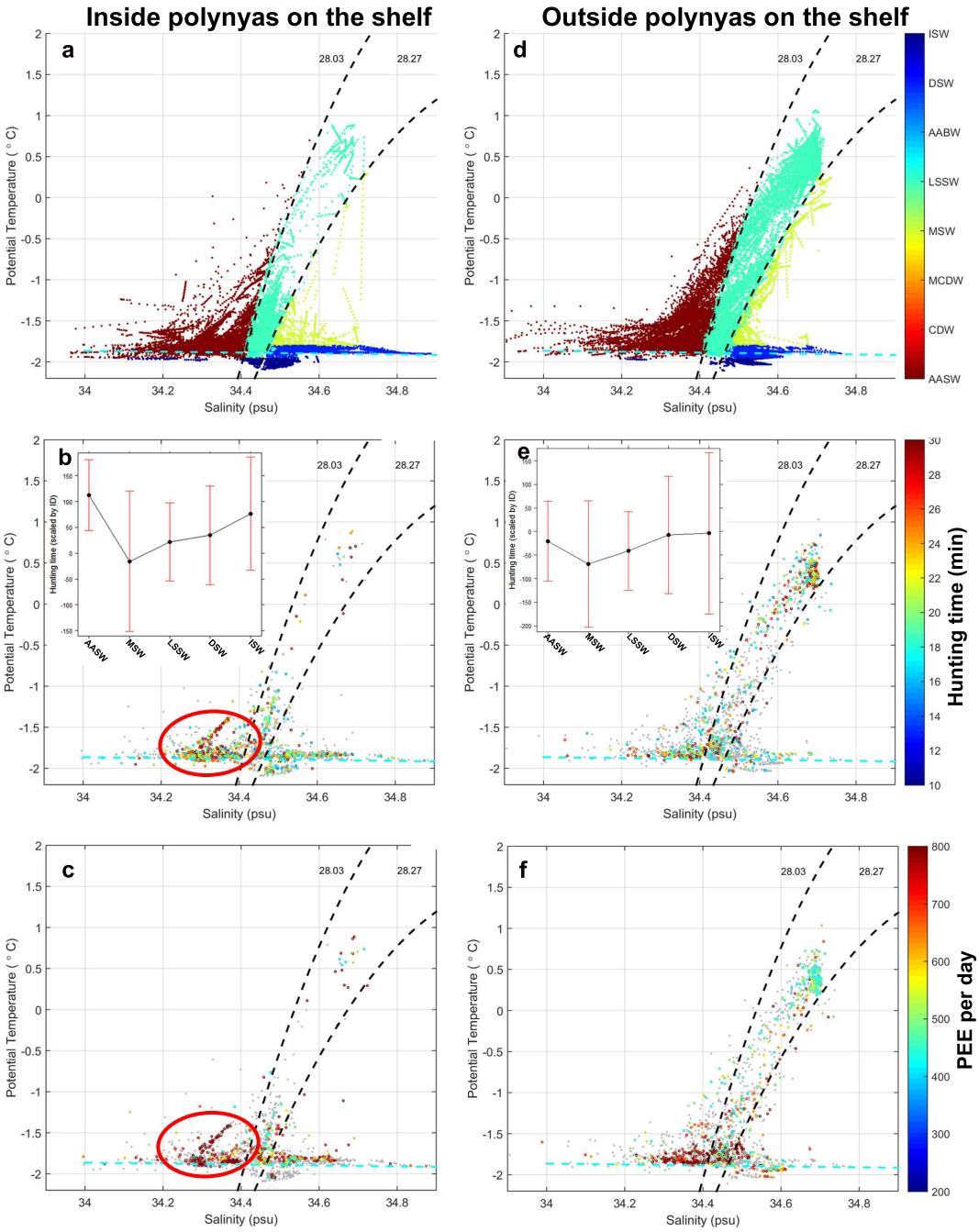


Figure V.7: Temperature salinity diagrams of hydrologic properties sampled by the 17 post-moult Kerguelen male SESs visiting the Antarctic shelf from 2004 to 2014 CTD casts. A total of 18 individuals visited polynyas however, CTD data were not available for the individual 2008-1. Left panels represent hydrologic properties inside polynyas, right panels represent hydrologic properties outside polynyas. Panel (**a**) and (**d**) represent all water masses sampled at the bottom phase of dives, acronyms and definitions of water mass classes can be found in Table V.1. Panel (**b**) and (**e**) represent hydrologic properties at the maximum depth of dives with colour scale representing the hunting time per dive (expressed in minutes). The offset represents the relationship from the LMM between hunting time per dive and water masses. Panel (**c**) and (**f**) represent hydrologic properties at the maximum depth of dives with colour scale representing predicted prey encounter events per day from behavioural models. Hunting times below 15 minutes and PEE per day below 400 are shown in grey as an attempt to highlight foraging hotspots. Figure from CTD data.

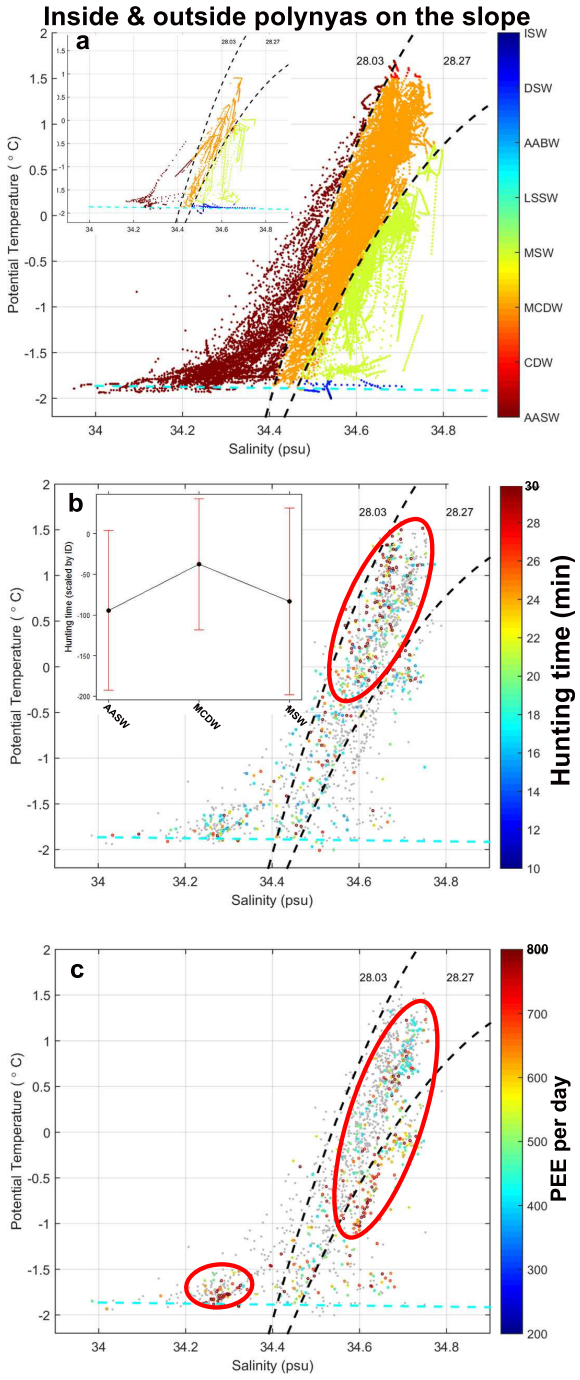


Figure V.8: Temperature salinity diagrams of hydrologic properties sampled by the 20 post-moult Kerguelen male SESs visiting the Antarctic slope from 2004 to 2014 CTD casts. Panel (**a**) represents all water masses sampled at the bottom phase of dives outside of polynyas and the offset represents water masses sampled inside polynyas on the slope region, acronyms and definitions of water mass classes can be found in Table V.1. Panel (**b**) represents hydrologic properties at the maximum depth of dives with colour scale representing the hunting time per dive (expressed in minutes). The offset represents the relationship from the LMM between hunting time per dive and water masses. Panel (**c**) represents hydrologic properties at the maximum depth of dives with colour scale representing predicted prey encounter events per day from behavioural models. Hunting times below 15 minutes and PEE per day below 400 are shown in grey as an attempt to highlight foraging hotspots. Figure from CTD data.

with regards to seals use of AASW in polynya. When investigating more seals diving behavior in AASW in polynya in June, it appears that they do not favor either benthic or pelagic dives, but perform both types of dives (Figure V.10f).

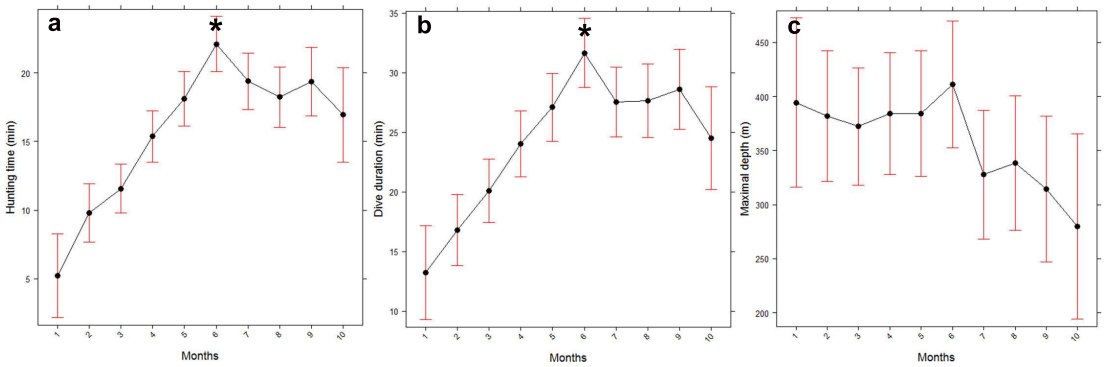


Figure V.9: Seasonality in the diving characteristics for the 17 post-moult Kerguelen male SESs inside polynyas from 2004 to 2014 CTD casts. A total of 18 individuals visited polynyas however; CTD data were not available for the individual 2008-1. Change in (**a**) hunting time, (**b**) dive duration (both expressed in minutes) and (**c**) diving depths (expressed by the maximal depth in meters) inside polynyas relative to months from 2004 to 2014 from the LMMs. Stars represent that the highest value is significant. Figure from CTD data.

An illustration of the time-series of a seal dive profiles associated with potential density, temperature, position relative to polynyas, foraging indexes and the stratification is represented in Figure V.11. The enters/exits in polynyas are represented by vertical blue lines (core 1) and green lines (core 2). We also represented the bathymetry associated with dives, dots connected by grey lines and colored differently between the shelf (red) and the slope (black). Early in the season, the seal dived below 500 m in warm and stratified waters. At the end of April, the seal entered for the first time the Cape Poinsett polynya and then interestingly successively exited and entered the polynya (vertical lines) alternating shelf and slope locations (red and black dots). During this phase, the water was stratified and the temperature sampled was cold except close to the bottom of dives where warmer temperatures were observed. The seal alternated shallow and deep dives (~ 300 to 800 m), reflecting benthic foraging activity on the slope and the shelf. Around mid-May, the seal exited the polynya and remained on the slope displaying similar dives in similar water characteristics. At the end of May, the seal entered again the polynya, however in contrast with previous periods, dives often reached 700 m and a destratification in surface waters (~ 100-200 m) was observed, presumably reflecting a phase of convection of the water column properties. The bottom of dives was still characterized by warmer water during the May/June transition. Simultaneously, an increase of foraging activity (hunting time and PEE) was observed inside polynya in late autumn/early winter (May/June). In June, the seal had a period of very shallow dives (~ 200 m) in the core 2 of the polynya followed by a period of constant dives at ~ 500 m inside the core 1 of the polynya, these dives were not benthic. From late June to mid-August, the seal remained on the shelf inside the different cores of the polynya and display both benthic dives at 500 m and a majority of shallow dives at ~ 250 m. From June

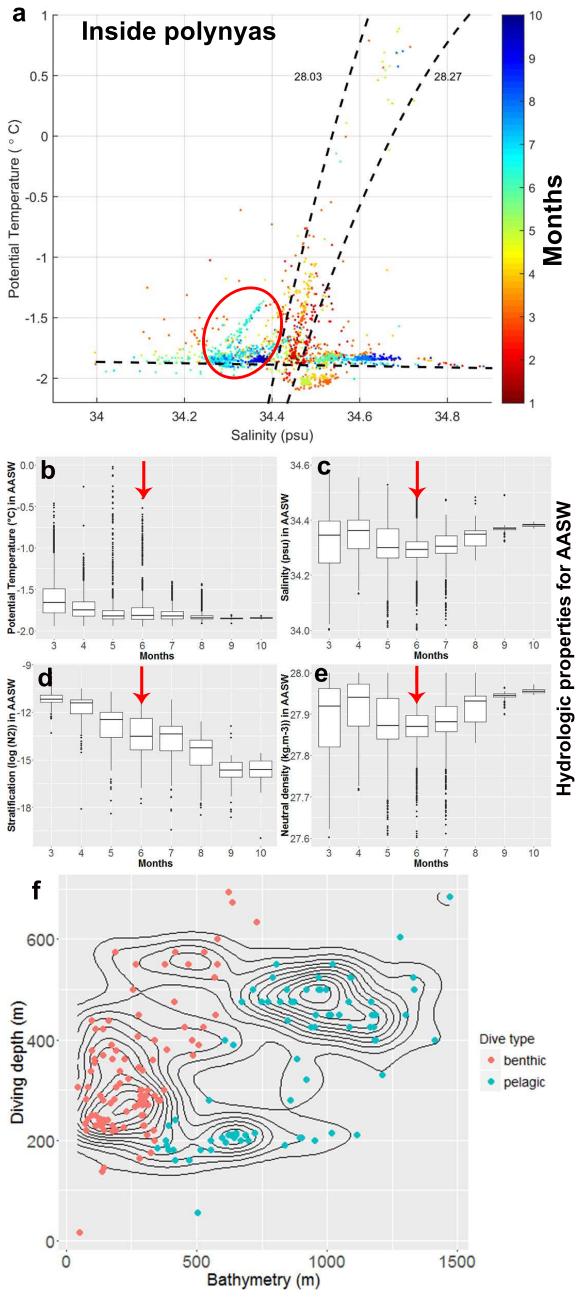


Figure V.10: Seasonality in the hydrologic properties at the bottom of dives inside polynyas sampled by the 17 post-moult Kerguelen male SESs from 2004 to 2014 CTD casts with a focus on the month of June for the AASW. A total of 18 individuals visited polynyas however; CTD data were not available for the individual 2008-1. Panel (**a**) represents TS couples sampled at the maximal depth of dives inside polynyas, color scale represents the months of the year from January to October. Hydrologic properties of the AASW relative to month of the year are represented in panel (**b**), (**c**), (**d**), (**e**), with potential temperature (expressed in °C) in panel (**b**), salinity (expressed in psu) in panel (**c**), stratification (expressed in log of N^2) in panel (**d**) and neutral density (expressed in $kg.m^{-3}$) in panel (**e**). The red arrows represent the month of June. Panel (**f**) represents the bottom diving depths (expressed in meters) relative to the bathymetry (expressed in meters) associated with each dive position of the 8 males inside polynyas in June and sampling the AASW. Contours represent the 2D kernel density estimation (*kde2D* function from package *MASS*, from R Development Core Team). Dots represent diving points colored in function of the dive strategy, benthic or pelagic. Figure from CTD data.

to August, the water column was homogeneous and characterized by cold temperatures. In mid-August, the seal exited the polynya and the shelf very quickly gaining warmer temperatures and spring stratified waters.

3.6 Influence of the polynya size and its variability on seals' polynya use and foraging activity

We investigated for each polynya the linkage between its maximal size (based on the larger contour of sea ice production) and the daily average of hunting times per dive and prey encounter events per day (Appendix D, Figure DX2). Qualitatively, no clear pattern was observed. We then investigated for each polynya the linkage between its size variability (based on the daily thin ice area divided by the maximum area based on the larger contour of sea ice production) and the daily average of hunting times per dive and prey encounter events per day (Appendix D, Figure DX3). Similarly, no pattern was observed.

4 Discussion

This study presents a novel quantification of the utilization of Antarctic coastal polynyas by a marine predator. We demonstrated that coastal polynyas in East Antarctica are a key winter habitat for SESs from Kerguelen Islands. Unique hydrological features were identified and may hold the answer to the causes underpinning seal use of coastal polynyas. Two different strategies polynyas utilization were observed among seals during the post-moult period which implied both post-polynyas and polynyas. This suggests that distinct peaks in resources availability may exist in polynyas over the season. In particular, the fall transition appears as a key moment in the winter foraging ecology of SESs, when polynyas may constitute a winter oasis for meso-apex predators.

4.1 General patterns of polynya use

Enhanced primary production in coastal polynyas [Arrigo and van Dijken, 2003], especially diatom blooms, appears to extend feeding and reproduction of secondary producers into late summer and early autumn (reviewed by Deibel and Daly [Deibel and Daly, 2007]), resulting in higher resources available for meso-apex predators inside polynyas during the post-moulting period of SESs (January – October). This presumably explain the marked increase in SESs foraging activity in polynyas and the large proportion of time they spent there, with an average 25 ± 20% (standard error) of their trip duration (and up to 75%). Details about the underlying oceanographic mechanisms involved in coupling between primary production, secondary producers and predators will be developed later.

The use of polynyas was notewhorthily divided into two strategies over the post-moult period of SESs: a first group (9 seals) spent relatively short time early in the season (January - April) in post-polynyas; while a second group (9 seals) remained in polynya during the

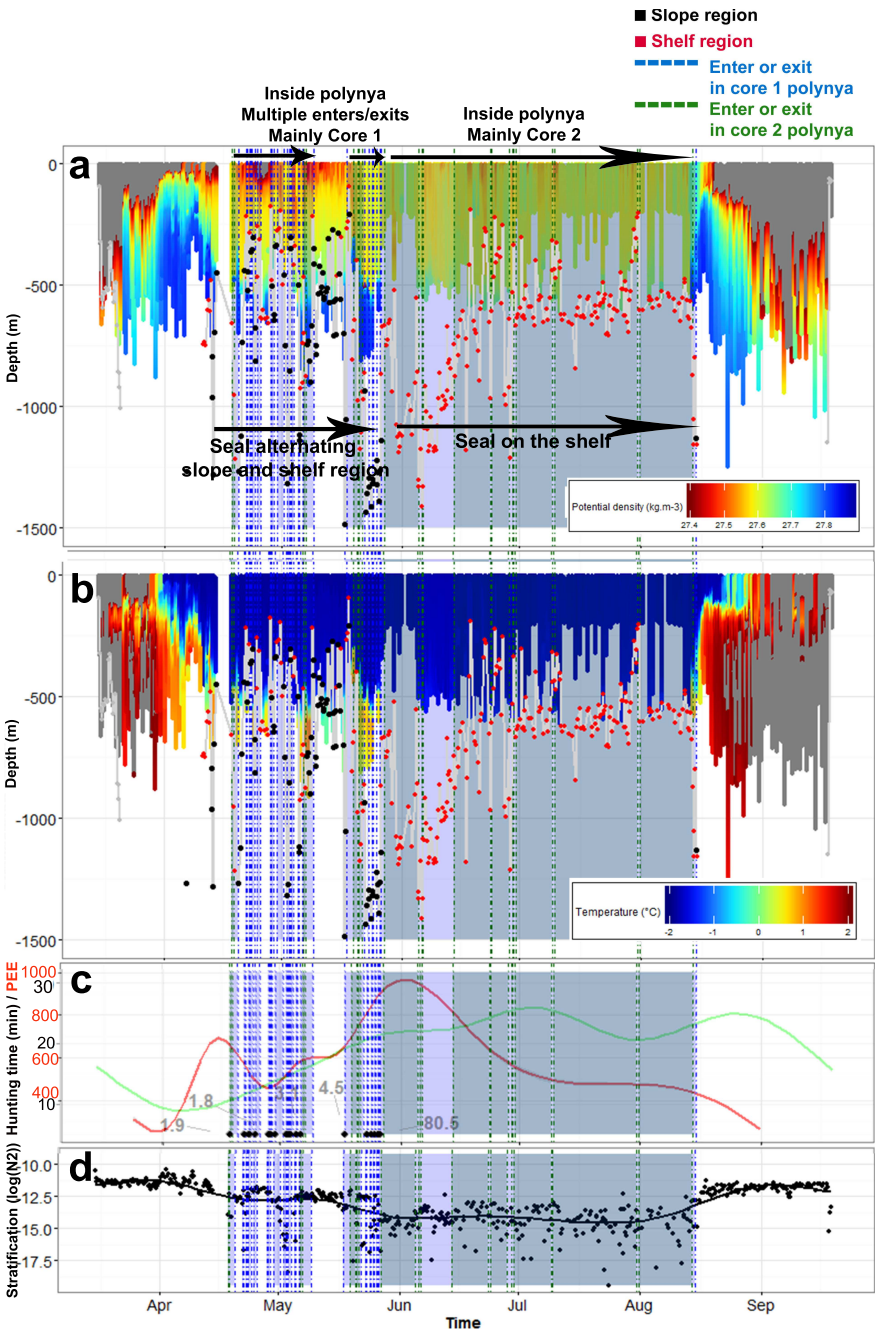


Figure V.11: Section combining dive information and hydrologic properties sampled by one individual in 2013 from March to September visiting the Cape Poinsett polynya. Panel (**a**) and (**b**) represent the time-series of dive profiles for the whole CTD cast, the color corresponds to the potential density and the temperature (only density from 27.4 to 27.9 kg.m^{-3} and temperature from -2 to 2°C are represented, the rest is grey colored) respectively. Red, green and grey dots linked by grey lines represent the bathymetry above 1500 m for the Antarctic shelf, slope and outside these regions respectively. Blue dashed lines correspond to enters and exits of polynya, blue fillings correspond to periods inside polynyas in the core 1 (2.5 m.y^{-1} of SIP), green fillings correspond to periods inside polynyas in the core 2 (5 m.y^{-1} of SIP). Panel (**c**) represent the smoothed time-series of two foraging index, hunting time per dive (expressed in minutes) in green and predicted prey encounter events per day in red. The number associated to each dots corresponds to the time spent in polynyas (only for time > 1 day). Panel (**d**) represents the time-series of stratification for each dive computed from the surface to the maximal depth of the dive (expressed in log(N^2)). Figure from CTD data.

winter (February – October). Early in the season, the freezing period has not started yet and seals of the first group may have taken advantage from enhanced biological activity from spring blooms in post-polynyas [Arrigo and van Dijken, 2003] but may have shortly headed up to different foraging areas. Seals of this group may be males avoiding the risk of being trapped in sea ice but still showing site fidelity to polynyas early in the season. In contrast, seals of the second group may have taken advantage of both open water access provided by polynya within dense pack/fast ice in winter, and prolonged secondary production in polynyas in contrast to surrounding sea ice covered waters. Interestingly, five seals of the second group were larger than the average male weight, and were perhaps more physiologically capable to survive in sea ice regions. Indeed, larger seals can presumably hold their breath for longer [McIntyre et al., 2010a], and may be able to break through the ice to breath [Hindell et al., 2016] when they travel from/to polynyas to/from the open ocean in winter.

4.2 Change in dive patterns inside polynyas and in the different sea ice production cores

SESs foraging activity was significantly higher and diving depth shallower in polynyas, and although seals spent most of their time in core 1 of the polynya, foraging activity and diving depth in core 2 (SIP between 5 and 10 m.y^{-1}) were significantly higher and shallower than in other cores. We hypothesize that strong sea ice production occurring in polynyas' core 2 is associated with open water or thin ice area with a relatively predictable access to the surface for SESs to breathe. In contrast, in polynyas' core 1, sea ice production is lower and this probably results in accumulation of thicker ice above 0.2 m which may constitute a constraint for seals. Shallower dives may presumably reflect the presence of prey resources in the upper surface layer in polynyas following extensive primary production in spring. Finally, only a small fraction of dives inside polynyas (6.7%) took place in core 3, and hunting times and diving depths there did not differ markedly from outside polynyas. We hypothesize that central waters of polynyas are not favorable to predators because they are the most deeply mixed due to extremely high sea-ice production. Several studies in the Ross sea polynya identified the south-central waters of this polynya as a virtual "desert" in terms of birds and mammals, while most top predators were observed in the marginal ice zone ringing the polynya [Ainley et al., 1984]. Waters in polynyas' core 2 may be preferred by SESs as they may harbor higher quantities of fish and krill than polynyas' central waters. Indeed, these well-lit waters often harbor more diatoms compared to central mixed waters, due to their higher nonlimited growth rate and resistance to photo-inhibition [Karnovsky et al., 2007]. Diatoms were found to dominate the phytoplankton community in the marginal ice zone of the Ross sea polynya and represented a major food source for krill [Quetin and Ross, 1985, Quetin and Ross, 1991]. In contrast, the genus *Phaeocystis* was found to dominate the more deeply mixed open waters of the Ross sea polynya due to an ability to grow faster at variable irradiance levels. From acoustic surveys, krill, the staple of the food chain, is presumably mostly confined to the edge of the marginal ice zone in

the Ross sea polynya [Azzali and Kalinowski, 1999], where it preferentially feed on diatoms over the genus *Phaeocystis* [Haberman et al., 2003]. These processes may explain why SESs foraged better in core 2 of the polynya instead of deeply mixed water in core 3, the former being probably associated with a diatom-based trophic chain based fuelling a higher secondary production.

4.3 Oceanographic conditions in polynyas

SESs foraged for longer in AASW inside polynyas, while they foraged similarly in all water masses encountered outside polynyas on the shelf. AASW was characterized by cold temperatures inside polynyas (below -1.5°C) and may be favorable for SESs by its potential negative influence on the movement capacity of SESs prey. As suggested by Bailleul et al. [Bailleul et al., 2007b], several physiological processes are reduced at low temperatures, including the contraction speed and power of locomotory muscles in aquatic vertebrates [Rome, 1990]. Although physiological adaptations to low temperature are found in the muscle functions of Antarctic teleosts [Johnston et al., 1975], very cold waters of polynyas, typically below -1.5°C, are likely to reduce fish speed [Claireaux et al., 2006].Thus, SESs may take advantage from the reduced speed of their prey in cold AASW present in polynyas.

The time spent in polynyas on the Antarctic slope was short, thus we studied the foraging activity combining both data inside and outside polynyas. Briefly, SESs had a longer hunting time in MCDW within the continental slope where intrusion of this water-mass brings relatively saline, warm and nutrient rich water onto the continental shelf stimulating primary and secondary production in the region [Prézelin et al., 2000]. Other benefits may also include the energy saved by staying in warmer water and moving with the flow [Williams et al., 2011]. These results were already seen for different SES population in two circumpolar studies [Biuw et al., 2007, Hindell et al., 2016] and two studies in East Antarctica [Williams et al., 2011, Labrousse et al., 2015].

4.4 The fall transition, a key point of the winter foraging ecology

Inside polynyas, AASW sampled in June by seals was characterized by the seasonal lowest salinity, and density and a plateau in the overall decay of stratification. A "V" shape was observed in the seasonal salinity and neutral density properties of the AASW (Figure V.10c and e). Arguably, this transition in oceanographic conditions is a transition between, first, the spring/summertime deepening of the cool and fresh surface layer, which is associated with a lowering of the AASW salinity and its destratification, and, second, the autumn/wintertime brine rejection associated with sea-ice formation, which is associated with increase of salinity and an even stronger destratification. In terms of seals behaviour, this transition was associated with the longest hunting time and dive duration and the deepest diving depth during the season inside polynyas. Williams et al. [Williams et al., 2011] reported a similar behaviour in post-moulting female SESs tagged in Macquarie Island and foraging in the Commonwealth Bay polynya. They hypothesized

that the continuous foraging activity observed within this polynya during the summer/fall transition (Feb-April) was due to favorable feeding conditions resulting from the convective overturning of the deep seasonal mixed layer and chlorophyll maximum. Indeed, in summer, the seasonal mixed layer forms above the past winter mixed layer and in some regions, deep seasonal mixed layer forms in conjunction with a deep chlorophyll maximum. At the end of the summer atmospheric cooling modifies the surface back to the freezing point, initiating sea ice growth and the development of the new winter mixed layer. During the fall transition, the deepening of the seasonal mixed layer entrains nutrients and/or mixes up the summer subsurface chlorophyll bloom (deep chlorophyll maximum), allowing phytoplankton production likely developing an autumn bloom [Thomalla et al., 2011, Chiswell et al., 2013]. We hypothesized that longer hunting times and dive duration, and deeper dives during the fall transition in polynyas may represent SESs taking advantage from enhanced secondary production from this autumn bloom. Moreover, while they dived deeper inside polynyas during this transition in June, no clear trend in the diving strategy (i.e. benthic or pelagic) was observed, suggesting that seals exploited the whole water column, displaying both benthic and pelagic dives with bimodality in the diving depth at ~ 300 and ~ 500 m in AASW.

The timing of this transition is described by Williams et al. [Williams et al., 2011] in April and Thomalla et al.[Thomalla et al., 2011] and Christwell et al. [Chiswell et al., 2013] described it between April and June but their studies took place at lower latitudes in the Southern Ocean. In the present study, it occurs in June. The timing of these processes depends on ocean-atmosphere interactions and the stratification of the upper water column in summer is influenced by the seasonal mixed layer properties and the presence/absence of MCDW [Williams et al., 2011]. We can thus hypothesize that regions with a deep/strong seasonal mixed layer and/or maximal inflow of MCDW may have a later start in the sea ice growth season and in turn the convective overturning of the deep seasonal mixed layer may probably be delayed from April to June as observed in the present study.

Finally, it worth to suggest that longer hunting times, dive durations and deeper dives could also represent difficulty in finding preys at this time of year, but during the winter months following the transition, if this hypothesis was true, we should observed an increased in these patterns. However, hunting times and dive durations decreased while dives became shallower, so this hypothesis may not be valuable.

4.5 Influence of polynya size

In the present study, we did not find any influence of the polynya size or its variability on the seals' use of polynya neither on their foraging activity. While different studies reported a greater abundance of marine mammals and birds in large productive polynyas [Arrigo and van Dijken, 2003, Karnovsky et al., 2007, Paterson et al., 2015], the mechanism by which larger polynyas may enhance primary production at the basis of the food chain is unclear. As detailed by Arrigo et al. [Arrigo et al., 2015], polynya size does not have a direct

influence on primary production neither via the mixed layer depth (as MLDs in different polynya size cases are similar), neither via nutrients availability, neither via sea ice melt releasing iron (as sea ice can also be advected away by winds and currents) and not even via light availability (as there is only a weak relation between open water area and photosynthetically usable radiation). Further studies are needed to establish potential linkages between polynya size and its influence on the ecosystem at all trophic levels.

5 Conclusion

Using a 11 year time-series obtained on 18 individuals tracked during their post-moult trip, we evidence for the first time that Kerguelen male SESs target Antarctic coastal polynyas and increase their foraging activity in polynyas in autumn and winter. Both post-polynyas during summer and polynyas from fall to the end of the winter season were used. Unique biological and physical features characterized polynyas as winter oasis for SESs, these are: (i) open water access to breathe at the surface throughout the winter; (ii) extended secondary production in late summer/fall from enhanced primary production; (iii) polynya sea ice growth leading to cold AASW with potential implications on prey mobility; (iv) a key fall transition resulting from the deepening of the seasonal mixed-layer, entraining the remnant deep chlorophyll maximum into the surface layer, presumably stimulating an autumn bloom and providing resources for predators in these winter sea ice covered areas.

It still remains unknown why five polynyas were more used than other. With this in mind, effect of inter-polynyas differences in oceanographic conditions, topography; proximity to the Antarctic Slope Front, and sea ice conditions on the seals' foraging performance should be investigated. No clear pattern was observed in the annual primary production of these polynyas based on Arrigo and van Dijken data [Arrigo and van Dijken, 2003]. Nevertheless, it should be kept in mind that seals may also choose polynyas from innate behaviours, e.g. opportunistic feeding when high prey patches are present, or predation avoidance and thus may remain in polynya as sea ice extends for the whole winter. The role of innate behaviours such as opportunistic feeding or predation avoidance is often overlooked when analyzing the foraging ecology of predators in relation to environmental conditions, which could sometimes lead to misinterpreting observed behaviours.

Finally, given the spatio-temporal complexity of the variations and processes involved in polynyas, it is difficult to predict how these key habitats will respond to climate change and variability. Following Arrigo et al. [Arrigo et al., 2015], phytoplankton biomass and primary production in coastal polynyas may increase in the future, as the melt of Antarctic ice shelves, releasing iron (explaining most of the variance in primary production in polynyas) is likely to increase in the future [Bell, 2008]. Thus, the ecological importance of coastal polynyas may increase as these regions will become even more favorable for the growth of both phytoplankton and the meso-apex predators such SESs that rely on them as a food source. Understanding the reliance of mesopredators upon particular sea-ice features contributes to deepening our much-needed knowledge on the under-ice biological habitat.

Acknowledgements

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GENERAL DISCUSSION, PERSPECTIVES AND CONCLUSION

6 Summary

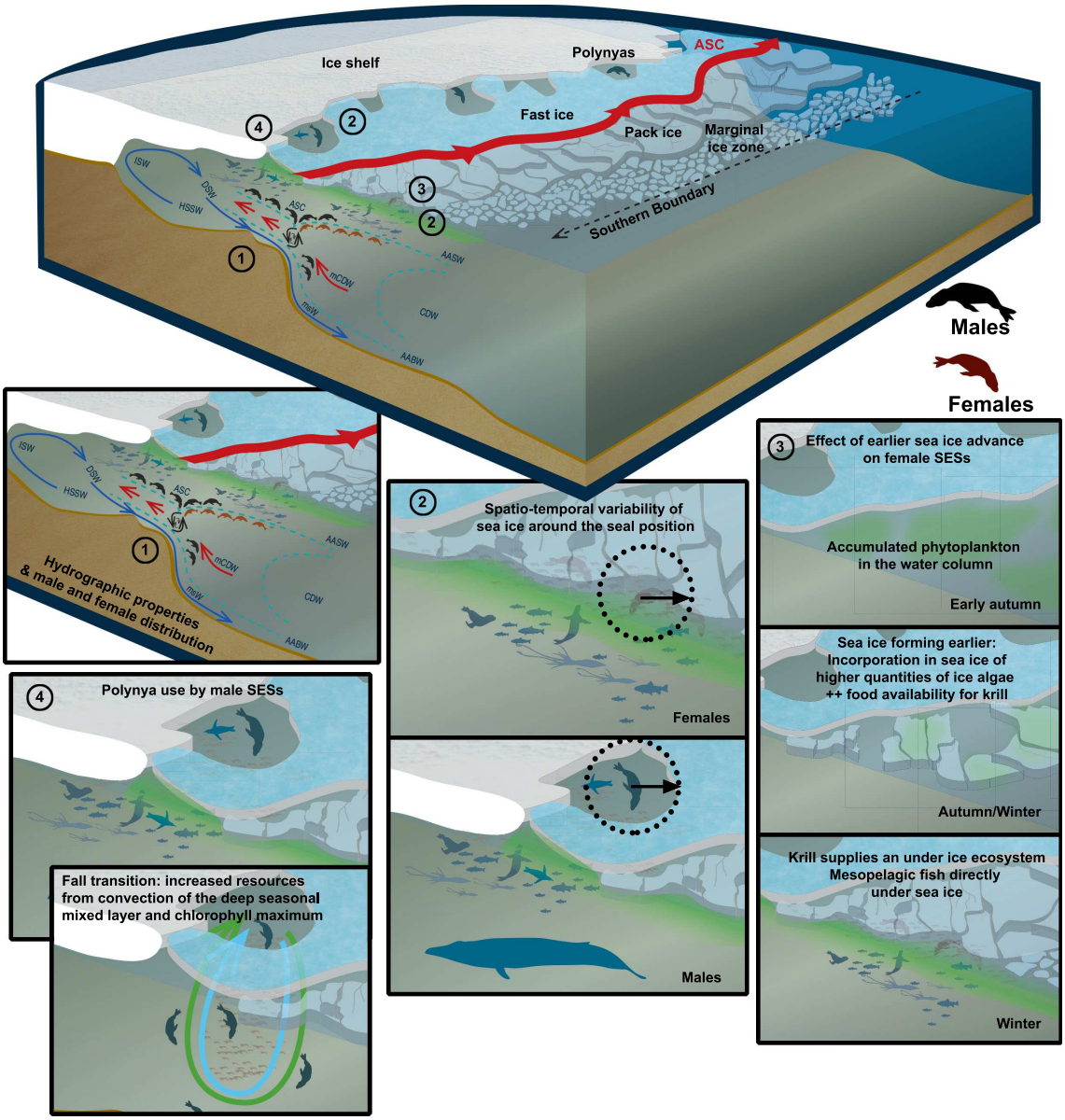

Figure CL1: Scheme synthesis of the four chapters of the thesis. Males southern elephant seals are represented in black while female southern elephant seals are represented in orange. The rough delineation of the Southern Boundary of the Antarctic Circumpolar Current and the westward Antarctic Slope Current are represented by the dashed black arrow and the red filled arrow respectively. The three types of sea ice are represented: the marginal ice zone, the pack ice and the fast ice.

In this thesis, an 11-year time-series (2004-2014) of southern elephant seal (SES) movements and diving behaviour corresponding of 286,843 dives collected by 23 females and 23 males was studied. These animals were chosen from the larger dataset because they visited the area south of 55°S, which is equivalent to the maximum latitude of annual sea ice extent

(in September). After their annual moult, males and females left the colony between late December and early March; females returned to the colony between September and October, and males between September and November for the breeding season. From the 46 tagged seals chosen, fourty-one individuals (19 females and 22 males) visited the Antarctic sea ice region and 18 males visited polynyas during their post-moult foraging trip at-sea.

The sea ice environment during winter is often considered as a "desert" in terms of re-sources. However, we showed that over multiple years, the food demands of large and abundant predators are met hundreds of kilometers deep into the pack ice throughout the dark winter months. The females were widely distributed with important foraging activity south of the Southern Boundary Front, while males predominately travelled to the south-eastern part of the East Antarctica region. Two general patterns of sea ice usage were observed according to sex: females remained in the outer part of the pack ice but tended to move with the ice edge as it extended northward. In contrast, males remained on the continental shelf/slope despite increasing sea ice. Demersal diving (Chapter II) represented only 8% of female's dives, compared to 35% of male's dives. Females spent 8 ± 13%, 20 ± 17%, 72 ± 25% of their time on the shelf (average ± standard deviation), slope and pelagic zones respectively (Chapter II). In contrast males spent 48 ± 27%, 22 ± 22%, 31 ± 25% of their time on the shelf, slope and pelagic zones respectively

Acting as an ecological double-edged sword, sea ice provides and concentrates a rich ecosystem during wintertime, while also presenting a physical barrier for air breathing predators. Several studies suggested that female SESs generally avoid the sea ice zone to prevent the risk of getting trapped by sea ice; however I have demonstrated that they were actually foraging for longer in the outer part of the pack ice compared to open ocean, 150 - 370 km south of the ice edge in late autumn (see Figure CL1). Within these persistent regions of compact sea ice, females foraged most intensively in the highest, but also highly variable ice concentration at and around their position (Figure CL1, insert 2). The high spatio-temporal variability of sea ice probably enabled females to exploit concentrated sea ice patches. Despite a lack of information on prey availability, females may exploit the ice algal autumn bloom that sustains an under-ice ecosystem including their mesopelagic prey. In the vertical dimension, females had longer hunting times over shallower seabed depths close to the Antarctic shelf and at the boundary between the overlying Antarctic Surface Water and the underlying Modified Circumpolar Deep Water (see Figure CL1, insert 1). They may take advantage of fish overwintering at the upper boundary of the Modified Circumpolar Deep Water.

In marked contrast, the males' foraging effort increased when they were deep within sea ice over the shelf (420 - 960 km from the ice edge; see Figure CL1). Although males remained on the continental shelf/slope throughout the winter, they foraged most intensively in the lowest and most variable sea ice (see Figure CL1, insert 2). Males had two distinct foraging behaviour: (i) pelagic dives within the Antarctic Slope Front on the continental shelf break where upwelling of nutrient rich Circumpolar Deep Water onto surface water may enhance and concentrate resources (see Figure CL1, insert 1); (ii) shallower pelagic and benthic dives

in equal proportion within coastal polynyas sustaining rich ecosystems throughout the ice season (see Figure CL1, insert 4). For the first time, I demonstrated that coastal polynyas in East Antarctica are true winter oasis for male SESs spending an average 25 ± 20% (SE) up to 75% of their total foraging trip in them. These permanently open water areas within sea ice covered regions often harbour the highest phytoplankton biomass on the already relatively productive continental shelf [Arrigo and van Dijken, 2003]. Being sites of concentrated biological activity, polynyas have the potential to support large populations of birds and mammals (e.g. emperor penguins, minke whales, crabeater seals, etc...) that can breathe and feed throughout the ice season. The autumn transition was a key moment in the winter foraging ecology of the seals with the highest foraging activity, dive durations and deepest dives observed inside polynyas (see Figure CL1, insert 4). A possible explanation for this enhanced foraging activity is that seals may have taken advantage of the secondary production resulting from the deepening of the seasonal mixed-layer, entraining the remnant deep chlorophyll maximum into the surface layer and presumably stimulating an autumn bloom.

Finally, I have highlighted the importance of near-surface meridional winds in effecting foraging activity of female SESs through their influence on the timing of sea ice advance (see Figure CL1, insert 3). We found that years with stronger meridional winds were associated with earlier sea ice advance with increased female foraging activity. This was in contrast to a previous study in the region west of the Ross Sea sector suggesting earlier sea ice advance would prevent females from accessing profitable prey patch areas on the shelf and slope sooner [van den Hoff et al., 2014]. These contrasting results in two different regions of Antarctica highlight the difficulty associated with simply extrapolating results from one region to another, and also underline the complex linkages between seal foraging performance and sea ice characteristics. I hypothesized that the early development and advance of sea ice in autumn would enhance primary production within the ice thereby providing increased resources for females within the ice in winter (through different trophic cascading effects; see Figure CL1, insert 3). Depending on the sea ice conditions in the different sectors of Antarctica, the benefit of having a well-developed community readily available earlier in the season could be negated by the increasing constraints for air-breathing predators associated with persistence in time and space of high sea ice concentrations around their positions. In the East Antarctic sector studied here, regionally complex patterns in sea ice seasonality have occurred over the past 30 years, with inter-annual sea ice duration anomalies subtler and generally less pronounced than in the Western Ross Sea where the increasing duration of the ice season has been particularly marked and uniform [Massom et al., 2013]. The timing of sea ice advance had only a weak effect on male foraging activity. More work is necessary to investigate the nature and drivers of inter-annual variability/change in key coastal polynyas, and their relationship with wind strength and direction, fast ice distribution and sea ice seasonality. Perhaps, once males are positioned in polynyas, wind-driven sea ice production and polynya size changes may not affect the prey availability or male foraging activity during the remainder of the winter season.

The plasticity of Kerguelen SESs in displaying two foraging strategies (frontal or Antarctic zones) suggests their ability to adapt to resource variability, which may help to explain the current stable population trend. For example, one strategy that favours energy gain over energy expenditure may be more advantageous, in terms of survival, for some years. In other years, another strategy that instead favours energy expenditure over energy gain, may be more advantageous. This plasticity can help buffer against individual mortality to improve overall survivorship of the population over the long term.

This work contributes to the better understanding of ecological mechanisms taking place in the little studied under-ice ecosystem, while elucidating a crucial part of the annual cycle of a major top predator of the Southern Ocean. The sustained monitoring of vertebrate colonies around the Antarctic coast and islands is crucial, given the complexity of the impact of climate forcing on biotic and abiotic components of the Antarctic marine ecosystem.

This part provided valuable information, which will help to answer the first and second objective of the thesis while also fulfilling the third objective. Indeed, we identified Kerguelen SES foraging strategies in the Antarctic sea ice region; understood how environmental conditions in the Antarctic sea ice region makes this region profitable in terms of resources and prey availability, and determined the difference between male and female strategies when seals foraged within the Antarctic sea ice region.

7 Alternate foraging strategies within a population: Antarctic versus frontal zones

As part of the second objective of the thesis, I proposed to document how foraging strategies of Kerguelen southern elephant seals in the Antarctic sea ice region compare with strategies in frontal regions of the Antarctic Circumpolar Current and discussed which factors may drive their choice.

Understanding why one individual SES chooses to forage either in the sea ice region or in frontal zones is a real challenge. Indeed, intra-specific differences between individual dive behaviour and distribution are well described in this, and other, sub-Antarctic species (e.g. [Charrassin and Bost, 2001, Arthur et al., 2016]), and likely arise from experience and personality, preferred prey type, metabolic requirements, prey capture technique, morphological capacity, predation or competition avoidance and the habitat available [Arthur et al., 2016]. Therefore, it is difficult to identify the causes underpinning individual seal decisions regarding foraging areas. However, once the foraging strategy (Antarctic or frontal zones) is selected, it is likely that seals will remain loyal to this type of foraging strategy throughout their lifetime. Indeed, Bradshaw et al. [Bradshaw et al., 2004] found that long-term fidelity to foraging sites may confer energetic advantages over an individual's lifetime and Authier et al. [Authier et al., 2012a] revealed how a stable foraging strategy developed early in life positively covaried with longevity in male SESs. Life-time reproductive

success, implicated when an individual shows strong site fidelity [Bradshaw et al., 2004], are likely to be met in both Antarctic and frontal zones, and both regions are likely to return (i.e. energy gain) on average similar returns over a seal's life, otherwise the less good foraging area would cease to be used over evolutionary time.

I hypothesised that the initial choice of foraging strategy between individuals and gender for SESs may be partly explained by the individual choice of prey, and prey distribution and availability. SESs dive deeper within the frontal zones and dives become shallower towards the Antarctic zone; diurnal dive variation are almost absent in the Antarctic zone, presumably due to feeding on prey remaining closer to the surface [Guinet et al., 2014] especially in sea ice covered-areas where the light is reduced or quasi absent in winter or likely due to benthic behaviour on the Antarctic shelf regardless of light [Biuw et al., 2007]. Another hypothesis to explain shallower dives may also be the positive influence of temperature at 200 m on the diving depth found by [Guinet et al., 2014]. Thus, decreased temperatures at 200 m towards the Antarctic continent may at least partially explain the presence of shallower dives. Highly shallow dives (< 40 m) were sometimes observed under high sea ice concentration in winter at night, where krill is suspected to be preyed upon by SESs [Walters et al., 2014]. Post-breeding female SESs, in frontal zones dived deeper during the day than at night and fed better when the temperature was under 8°C [Guinet et al., 2014]. The authors suggested they follow their main prey, myctophid fish, known to display diurnal vertical variation [Koubbi et al., 2011] and the 8°C isotherm is likely to represent the upper limit of their vertical distribution.

Generally, within the Southern Ocean, SESs foraging activity is associated with two types of processes both encountered in the frontal and Antarctic zones:

- a bottom-up process associated with a local nutrient enrichment from the horizontal or vertical advection of nutrients-rich water masses (e.g. iron), leading in turn to enhanced biological activity and resources, profitable for SES foraging activity;
- a process aggregating prey associated with thermal discontinuities or light level.

In the following sections, I first identified similarities and differences in the biophysical attributes driving these two processes between the frontal versus Antarctic zones for SESs and other sub-Antarctic species. In a second time, I discussed how these two strategies are maintained over time for the same species and what drives the choice of strategy. The two strategies and their main characteristics for SESs are summarised in the Table V.3.

7.1 Comparison of biophysical drivers

I divided biophysical drivers into three types: bathymetrically-entrained structures; oceanic fronts; eddies and filaments.

7.1.1 Bathymetrically-entrained structures

On the one hand, bathymetry-associated oceanographic processes may create stable micro-niches with enhanced resources through upwelling of nutrients [Bouchet et al., 2015] reducing the search time of predators and providing different energy content prey from deeper and colder waters [Scheffer et al., 2016]. This is a bottom-up process. On the other hand, discontinuities in physical properties of the water column within these structures leads to enhanced biological activity through an aggregation process [Lima et al., 2002].

During the austral winter, juvenile male SESs remaining in the vicinity of Kerguelen Islands were found to have a higher foraging activity within the Kerguelen shelf break, seamounts or ridges associated with enhanced biological activity compared to surrounding waters [O'Toole et al., 2014]. Similarly, incubating and brooding king penguins from Isles Kerguelen were found to forage in areas of bathymetrically-entrained cold winter waters south-east of Kerguelen, where upwelling of nutrients and creation of sub-surface thermal gradients [Charrassin et al., 2004, Scheffer et al., 2016] aggregate resources such as myctophids [Pakhomov et al., 1996]. For incubating birds, rugged bathymetry and seamounts are likely responsible of the upwelling of cold winter water while for brooding birds the cold water current are likely directed into the Kerguelen plateau by the shelf break. Similarly, King penguins breeding at Heard Island, macaroni penguin and Antarctic fur seals breeding at Heard and Kerguelen Islands were also found to forage in the areas within the Fawn Trough Current cold water flow likely interacting with the Kerguelen shelf [Goldsworthy et al., 2010, Hindell et al., 2011, Thiebot et al., 2014].

The importance of bathymetry-associated oceanographic processes have been shown in the present thesis with male SESs foraging intensively within the Antarctic Slope Front (ASF) or Current (ASC). The ASF corresponds to the strong subsurface horizontal temperature and salinity gradient separating the lighter AASW from the denser MCDW [Meijers et al., 2010]. This topographically constrained structure is likely a deep ocean source region for nutrients [Jacobs, 1991]from upwelling of Circumpolar Deep Water (CDW), resulting in higher productivity and enhanced and aggregated resources.

7.1.2 Oceanic fronts

Predators are also often associated with oceanic fronts, likely due to concentration of prey and nutrients by convergences processes or through physical discontinuities [Bost et al., 2009]. For example at the Polar Front, cold waters sink below the relatively warm sub-Antarctic waters where neckton actively stay and aggregate in the surface waters.

Within the frontal zones of the Antarctic Circumpolar Current (ACC), penguins and seals dive within and below the thermal discontinuity separating the seasonal mixed layer from the underlying waters in summer (i.e. thermocline) [Charrassin and Bost, 2001, Guinet et al., 2014, Scheffer et al., 2016]. Discontinuities in physical properties of the wa-

ter column may lead to enhanced biological activity by aggregation of some prey limited by temperature optimum (e.g. myctophids), or by density gradients building a barrier aggregating sinking organic matter. King penguin breeding at Crozet and South Georgia use prey within or close to thermal discontinuities in the vicinity of oceanic fronts during the summer season [Charrassin and Bost, 2001, Scheffer et al., 2012]. As mentioned earlier, foraging activity of post-breeding female SESs from Kerguelen was associated with water temperature at 200 m and light levels [Guinet et al., 2014] that are likely to effect the distribution of their prey within the frontal zones. Very few seals foraged in the region north of the Sub-Antarctic Front (SAF) where deepening of isotherms leads to warmer sub-surface waters; the SAF is therefore likely an important biogeographic boundary in the distribution of this species. Similar results were found in a circumpolar study by Biuw et al. [Biuw et al., 2007] with a seals' preference for frontal zones of the ACC associated with upwelling of CDW (especially for the South Georgia population in the Atlantic sector) and relatively few individuals visiting the areas north of the SAF.

In the Antarctic zone, female SESs were distributed south of the Southern Boundary of the ACC and foraged at the frontier between the cold Antarctic Surface Water (AASW) and the relatively warm modified CDW (mCDW), likely important overwintering areas for mesopelagic fauna.

Similarly to the SAF, the Southern Boundary of the ACC may also be a biogeographic frontier in the distribution of many species. Enhanced biological activity was found south of the Southern Boundary rather than in association with it, suggesting this boundary delineates a productive region by controlling the sea ice cover extent and its associate primary and secondary production [Nicol et al., 2000b]. The highest concentrations of blue, humpback, fin and minke whales were found south of the Southern Boundary [Tynan, 1998, Nicol et al., 2000b, Ainley et al., 2007].

7.1.3 Eddies and filaments

At mesoscales, eddy vorticity creates local upwelling and downwelling which lead to the aggregation of prey (i.e. aggregating process); for example myctophids were found along the edge of warm anti-cyclonic eddies which concentrated a high biomass of zooplankton and micronecton [Olson and Backus, 1985, Pakhomov and Froneman, 2000]. Indeed, in decaying warm-core eddies crustaceans prey (e.g. copepods) may move to the surface to remain at their optimal temperature. Using Lagrangian analysis, Cotté et al. [Cotté et al., 2015] also identified bottom-up processes where post-bloom waters advected by the ACC and trapped in eddies might allow the development of ecosystems in these features cascading up to higher trophic levels.

SESs use cold-core cyclonic eddies where upwelling of nutrients takes place at the centre, and high productivity and aggregation of prey take place at the edge [Bailleul et al., 2010b, Dragon et al., 2010]. A more recent study of [Cotté et al., 2015] within the frontal zones (including the Kerguelen Plateau) identified that post-moult female SESs

travelled along thermal fronts, where changes in water temperature associated with cold filaments (i.e. sub-mesoscale feature) may act as environmental cues to locate eddies, with higher prey densities [Benoit-Bird et al., 2013]. Structures such as filaments may also promote seal activity [De Monte et al., 2012] and enhance foraging by carrying high zooplankton densities [Perruche et al., 2011]. Cotté et al. [Cotté et al., 2015] suggested that water patches within eddies tracked by seals were post-bloom waters advected by the ACC, where the prey field likely developed and aggregated during the transport. Other species such as grey-headed albatross (*Thalassarche chrysostoma*) concentrated their foraging activity at the edge of eddies, especially warm-core eddies where they caught fish and squid, themselves predators of myctophids [Nel et al., 2001]. King penguins breeding in Crozet also used the edge of cyclonic eddies, as well as enhanced concentrations of prey at shallow depths in anti-cyclonic eddies due to an elevation of isopycnals [Bost et al., 2009]. However, king penguins may also use currents linked with eddy activity as oceanographic cues to find physical discontinuities of the water column in frontal zones [Bost et al., 2009].

Finally, a recent study of Dellapenna et al. [Della Penna et al., 2015] using a Lagrangian approach revealed that SESs display quasi-planktonic behaviour, drifting horizontally in eddies and fronts, and these periods corresponded with increased foraging efforts. This suggests that eddies and frontal structures may have a triple role with both a bottom-up and aggregating effects and a top-down effect by directly entraining trajectories of foraging seals. It is important to note that this quasi-planktonic behaviour may not be associated with reduced energy expenditure as seals increased their diving effort.

In the Antarctic zone, the thermo-dynamic destabilisation of the ASC creates a multitude of eddies. However, the ASC is poorly known especially during winter due to the presence of sea ice cover. Moreover, the small scale of the eddies, meanders and jets associated with the ASC (typically less than 10 km, and small down to 1–2 km) make observational studies challenging [Heywood et al., 2014]. The review of Stewart and Thompson [Stewart and Thompson, 2013] highlights the important role of eddies in the ASC in providing a bi-directional exchange across the Antarctic slope of heat, freshwater, nutrients such as iron or larvae and other biota [Heywood et al., 2014]. These structures may allow the development of an ecosystem and may also aggregate some prey, making them favorable foraging zones for SESs. This thesis described increased foraging effort of male SESs within the ASC, but further research is needed to investigate if SESs also use these mesoscale features as they do in eddies formed in frontal zones around Kerguelen.

One question arises: do SESs in the Antarctic zone adopt a quasi-planktonic behaviour within the strong ASC ? I suggest that the ASC, predicted to intensify during winter through wind induced-change in surface height along Antarctic coasts via Ekman drift [Mathiot et al., 2011], may also provide increased biological activity (i.e. bottom-up process) [Nicol et al., 2000b, Nicol et al., 2000a] and passive transport of SESs within it (i.e. top-down process). Williams et al. [Williams et al., 2011] have reported a potential quasi-planktonic behaviour of one SES within the ASC, however I have observed that meridional movements of male SESs exploiting the ASC were eastward rather than west-

ward, which is against the current. Finally, SESs may use the inflow penetration of warm, saline mCDW onto and across the continental shelf break as a preferential pathway into the continental shelf region benefiting by being moving with the flow reducing energy expenditure [Williams et al., 2011]. I observed that seals use mCDW within the continental slope and more research is needed to investigate if they follow the flow using a quasi-planktonic behaviour as suggested by Williams et al. [Williams et al., 2011].

7.2 Frontal or polar foraging: a trade-off

The choice by SESs of the frontal versus the Antarctic strategy may firstly depend of the type of foraging trip; post-moulting or post-breeding. During long post-moult trip of SESs (~ 8 months), SESs may have the choice between the two strategies while for shorter summer post-breeding migrations (~ 2 months), SESs from sub-Antarctic colonies distant from the Antarctic continent such as Macquarie and Kerguelen may be restricted to the frontal zones including the Kerguelen Plateau closer to the colonies.

For the Kerguelen SESs, the two strategies persist in the population suggesting that neither strategy will offer a significant benefit in the long term. However, Authier et al. [Authier et al., 2012b] found that females foraging in Antarctic waters weaned larger pups than females foraging in the inter-frontal zone [Authier et al., 2012b] conferring a benefit in terms of pup survival. But this is also a riskier strategy because inter-annual variability in sea ice may lead in some years to the presence of consolidated and constraining sea ice for breathing predators foraging in these areas, so this region may not provide good foraging every year. This may explain why the two strategies persist over time; the lifetime foraging success of females (reflected in the pup production) is likely to be the same for both strategies. It is still unknown if individual strategy is heritable or not, and even if differences between prey type and availability may guide the choice of foraging areas, the role of animal personality and experience may be preponderant. Experience factor is commonly neglected in ecological studies but may be responsible of the maintenance of the two strategies over years [Réale et al., 2007] and of the strong feeding area fidelity [Bradshaw et al., 2003]. Finally, we know almost nothing about how marine predators find their way using the oceanographic/physical/chemical cues found in frontal or Antarctic zones, or how at a finer scale, they adjust their search to find prey. A wide range of methods used by birds to navigate have been studied (e.g. [Nevitt, 2008]). Similarly, seals may also use a suite of methods to navigate in the marine environment. For example their chemo-olfaction capabilities [Sticken and Dehnhardt, 2000] may be used to detect different water masses due to their heightened sense of salinity in the water column. Furthermore, Kowalewsky et al. [Kowalewsky et al., 2006] suggested seals possess high olfactory sensitivity for dimethyl sulfide, a product derived from the grazing of phytoplankton by zooplankton, that may act as a chemical cue for productive areas.

Other sub-Antarctic species have similar diversity of foraging strategies. Forty percent of winter foraging trips of Marion Island Antarctic fur seals occurred at or south of the Polar Front and 47% in frontal zones in the vicinity of Marion Island [Arthur et al., 2016]. Half of animals dived in the same region during their winter foraging trips while the other half dived in the two regions, thereby combining both strategies. As Antarctic fur seals target vertically migrating prey at the surface at night, there is an advantage to foraging in southern waters as the duration of night (and therefore the duration of shallow diving) increases with latitude in the austral winter. The resulting and shallower dives may be associated with higher net energy gain than longer, deeper and more energetically costly dives in frontal zones. Similarly, short tailed shearwaters (*Puffinus tenuirostris*) change their foraging strategy seasonally. From the end of the winter to early summer, they mainly foraged within the Polar Front while as summer advances, shearwater distribution shifted southward close to the sea ice edge. As sea ice retreats, shearwaters forage over the Antarctic shelf. This southward shift corresponds with the hatching period associated with an increased in energy demand, and is perhaps compensated by enhanced resources within the marginal ice zone [Woehler et al., 2006]. King penguins breeding at Crozet, also change their foraging activity from the Polar Front in summer to the ice edge in autumn and winter [Charrassin and Bost, 2001]. Enhanced biological activity is found at the sea ice edge even in autumn and winter due to sea ice melt and breakdown releasing an important quantity of food resources (i.e. ice algae) under a strong influence of wind action and ocean wave-ice interaction processes (see discussion in chapter III for references).

To conclude, the plasticity of Kerguelen SESs and other sub-Antarctic species in exhibiting two foraging strategies (frontal or Antarctic strategies) may confer an advantage to the population in years when one of the two strateges is unfavourable and affect individual survival.

8 Comparison across southern elephant seal population

The first objective of the thesis was to understand the current stable status of the Kerguelen population by studying how environmental conditions modulate i) the availability of resources and, in turn, ii) their foraging strategy to compare with other observed population trends in different regions of the Southern Ocean. Here, I briefly discussed the different strategies adopted among the different populations of SESs and how the strategies adopted by the Kerguelen population may explain their current stable status, and shed some light on factors that may be contributing to trends at other sites.

8.1 Broad-scale habitat use of southern elephant seal population

All populations use both deep ocean and shelf regions, but with regional differences in the relative proportions. Regarding the South Georgia SES population:

Table V.3: Table summarizing the different characteristics of the frontal versus Antarctic strategies of southern elephant seals from Isles Kerguelen

Type of strategy	Sex	Prey item	Prey accessibility / Diving strategy	Hydrographic / sea ice properties	Main other species
Frontal strategy	Female adults	Myctophids, squids	1. Deep and long dives (500-600 m); Diurnal variation	Importance of the isotherm/isolume; regions of upwelling of nutrients and physical discontinuities in the vertical and horizontal dimension	Antarctic fur seals, macaroni and King penguins
			2. Target temperature at 200 m not exceding 8°C 2. Deeper dives in subtropical waters (deepening of the isotherm)		
			3. Use of cold filaments (i.e. sub-mesoscale feature) as environmental cues to reach eddies (i.e. mesoscale feature)	Submesoscale and mesoscale features	
			3. Feeding activity during the transport on high zooplankton aggregation	Post-bloom waters rich in nutrients advected by the ACC where prey field likely developed and aggregated during the transport	
			4. Display quasi-planktonic behaviour within eddies 4. Moving passively - Intensively diving & foraging		
Kerguelen Plateau	Male juveniles		Benthic dives	Bathymetrically entrained structures such as shelf break, seamounts ridges - prey aggregation and upwelling of nutrients	Antarctic fur seals, macaroni and King penguins
Antarctic strategy - MIZ & PIZ	Female adults	Myctophids, squids, krill	1. Shallower dives (400m) close to the Antarctic shelf break; presence of shallow dives presumably under sea ice (< 40 m) representing 4 ± 5 % of female dives within sea ice	Target the boundary between AASW and MCDW, overwintering areas of mesopelagic preys	King penguins, Antarctic fur seals, killer, minke, humpback whales
			2. Intensification of foraging activity in high sea ice concentration patches at their position but in spatio-temporal variable sea ice around them	Females may exploit the ice algal autumn bloom that sustains meso-pelagic prey in the under-ice ecosystem	
			3. Years of stronger meridional winds and earlier sea ice advance favoured their foraging activity	Early forming sea ice may incorporate more sea ice algae and lead to ice algal autumn bloom and secondary production associated with it	
Antarctic strategy - Shelf & Shelf break - FIZ, polynyas	Male juveniles	Notothenoids, squids, krill?	1. Pelagic dives within the Antarctic Slope Current	Bathymetrically entrained structures with prey aggregation and upwelling of nutrient-rich MCDW in AASW	Emperor penguins, crabeater, weddell, leopard seals, killer and minke whales
			2. On the shelf outside polynyas, mainly benthic dives		
			3. On the shelf inside polynyas, benthic and pelagic dives, dives in general shallower than in the shelf	Characterised by cold AASW - Open water areas within sea ice harbour high primary and secondary production likely to support air breathing predators throughout the ice season	
			3. Males spent in average 25 ± 20% of the time of their total trip inside polynyas and up to 75%		
			3. Hunting time and dive duration peaks and dive depth deepened in June	Fall transition in polynyas: access to prey from autumn bloom and secondary production created by the convection of the deep seasonal mixed layer entraining the remnant deep chlorophyll maximum into the surface layer	

- Sub-populations close to the Antarctic Peninsula or from South Georgia Island but tagged at their moulting sites (see Figure I.18; 2b. Falkland Island, 2c. South Orkney Island, 2d. South Shetland Islands including Livingston Island and Elephant Island) use Antarctic waters along the shelf and shelf break west of the Antarctic Peninsula or in the Bellingshausen Sea where males and females were found to remain across the four seasons (including both post-breeding and post-moulting trips) despite increasing sea ice;

- Sub-populations further away from the Peninsula (see Figure I.18; 2e. Gough Island, 2f. Bouvet Island) foraged within the ACC [Biuw et al., 2007, Hindell et al., 2016].;

During the first period of the post-moult season (February-April) South Georgia seals has a relatively high usage of the ACC (± 90% of the area restricted search (ARS) were localized in deep ocean while only 10% on the shelf [Hindell et al., 2016]) compared to Kerguelen and Macquarie populations (Indian and West Pacific sector) [Biuw et al., 2007] for which half of the ARS were in deep ocean [Hindell et al., 2016]. The ACC in the Atlantic sector was found to have high primary production due to iron provision from sediments in coastal margins and its horizontal advection at fronts and presumably the upwelling of nutrients-rich CDW from North Atlantic. This primary production develops where the western boundary currents detach from the continental shelves and turn eastwards into the Southern Ocean [Graham et al., 2015]. Although similar processes were described in the vicinity of shelf regions in the Indian sector and in the West Pacific, these regions are smaller than in the South Atlantic sector, which may explain the difference in seal use. During the rest of the post-moult periods (May-October), the proportion of the shelf ARS decreased for the Kerguelen population and were totally absent for the Macquarie population that stopped using the shelf region at this period [Hindell et al., 2016]. The seals from Macquarie travelled twice as far to reach the Antarctic shelf compared to sub-populations of South Georgia. This leads to an important additional energy expenditure compared to the other colonies.

8.2 Suggestions to explain the different demographic trends

As detailed in the section 5.2, the energy intake during winter foraging trips influences both pup mass at birth and at weaning and the subsequent survival of the pups in the first years of their life [McMahon et al., 2003, McMahon and Burton, 2005]. This early investment period has important consequences at the population level as juvenile survival is an important determinant of population growth rates [McMahon et al., 2005]. The average energy gain over the lifetime of an individual is likely to be equal between the less riskier, less rewarding frontal strategy compared to the high rewarding, but riskier, Antarctic strategy.

I hypothesized that the current stable status of the Kerguelen and South Georgia population may be explained by the plasticity within each populations to forage in two different habitats as described in the previous section 7.2. The two strategies may be partitioned

between individuals providing an advantage for one or the other sub-population in case of resources availability changes in one of the habitats. In contrast, seals from the decreasing Macquarie population visited the Antarctic shelf less and the the deep ocean more, thereby avoiding sea ice covered regions. A reduced Antarctic strategy in this sub-population may be highly disadvantageous especially in years where resources are less abundant in deep frontal ocean regions.

Sea ice conditions may represent a key factor explaining trends in SES populations in the Southern Ocean. As detailed in the section 4.7.1, contrasting sea ice trends are observed at the regional scale with increased sea ice coverage in the western Ross Sea (i.e. West Pacific sector), strong decreased sea ice coverage in the Bellingshausen and Amundsen seas (i.e. East Pacific sector) with related trends in yearly duration [Liu et al., 2004, Stammerjohn et al., 2012]. In the Indian Ocean, sea ice seasonality is subtler and characterised by mixed patterns at regional and local scales [Massom et al., 2013]. These differences between sectors in sea ice conditions may lead to (i) either inaccessibility of the Antarctic sea ice regions, thereby preventing seal from finding open water access to breathe (e.g. in the Ross Sea for Macquarie SESs), or (ii) being beneficial in terms of resources availability when conditions allow seal penetration within sea ice (e.g. in the Indian Ocean for Kerguelen SESs or in the Antarctic Peninsula for South Georgia SESs) [Hindell et al., 2016]. In the Western Antarctic Peninsula, pronounced decreases in sea ice extent lead to the presence of inlets, fjords, tide cracks and leads, allowing South Georgia SESs to exploit the shelf habitat for the longest time among the different SES populations. However, continuing sea ice reduction in the Western Antarctic Peninsula may reach a point that could negatively affect regional primary and secondary production, and in turn, SES resources. Finally, the Weddell Sea has been rarely used despite being located within reaching distance of South Georgia SESs. Heavy and dense pack ice might prevent the use of this region, as is the case in the Ross Sea that is expected to have implications for the Macquarie population.

Sea ice conditions in each sector are likely to influence, within SES populations, the existence of the Antarctic strategy complementing the frontal strategy. Like I have shown for the Kerguelen population where I identified strategy plasticity leading to stable or increased demographic trend, I suggest that it is also the case for other SES populations. Within a population, intra-individual adoption of one of two foraging strategies is expected to buffer against potential environmental changes that would otherwise impact overall population trend.

9 Foraging beneath sea ice: a double-edge sword

A diversity of foraging strategies exist in other air-breathing predators to take advantage of the resources of the Antarctic sea ice zone despite its breathing constraint. Below is a non-exhaustive list of examples of behaviour found within the Antarctic sea ice zone for four Antarctic species: crabeater seals, minke whales, Weddell seals, and emperor penguins.

9.1 Crabeater seals

Crabeater seals in Marguerite Bay (Western Antarctic Peninsula) foraged in areas with higher than average but not complete sea ice cover likely to be associated with higher krill density, but still allowing an access to air to breath or ice to rest [Burns et al., 2004]. Moreover, studies of Burns et al. [Burns et al., 2004] and Nachtsheim et al. [Nachtsheim et al., 2016] in the Western Antarctic Peninsula and in the Eastern Weddell Sea showed that crabeater seals make shallow and short dives at the surface during summer/autumn but deeper and longer dives during the winter/spring. They also changed their distribution from open ocean in the vicinity of the shelf break in summer/autumn to the continental shelf in winter/spring. The seasonal differences in diving patterns and distribution reflect the change in prey distribution, in this case, Antarctic krill. **No marked seasonal changes in diving behaviour and foraging habitat visited was observed for SESs studied in this thesis except in polynyas. Male SESs usually go straight to their preferred habitat and remained there for the whole winter. In contrast females remained in the pack ice while following the sea ice edge, but there were no pronounced changes in their diving behaviour.**

9.2 Minke whales

Similarly, the distribution of minke whale in autumn in Marguerite Bay was strongly associated with zooplankton abundance, itself tightly coupled with areas of high bathymetric slope [Friedlaender et al., 2006]. They follow their prey through aggregating oceanographic processes: in years when the sea ice does not fully retreat, krill and whales may aggregate at the sea ice edge. In years when sea ice fully retreats, whales may be found in areas of bathymetric structures such as the shelf break, seamounts or ridges which cause high velocity coastal currents that aggregate krill [Friedlaender et al., 2006]. Moreover, the relatively small body size of minke whales facilitates access to sea ice and the search for krill [Friedlaender et al., 2014]. This supports a niche not used by other krill predators such as other whales, seals, penguins and seabirds [Friedlaender et al., 2011]. The foraging strategy adopted by minke whales to feed at high lunge rates with relatively low energy expenditure (given their small gulps) compared with larger rorquals (committed to larger gulps time and energy consuming for filtering and processing the food) confers an energetic efficiently for dense, patchily distributed prey [Friedlaender et al., 2014]. **The use of the continental shelf break by minke whales underlines the importance of this region for predators, as described for male SESs in aggregating the resource while presumably providing sea ice conditions suitable for air-breathing predators.**

9.3 Weddell seals

Weddell seals breathe through holes in year-round fast ice [Kooyman, 1981], and with emperor penguins they are the only two warm-blooded predators using the Antarctic fast ice during winter [Burns and Kooyman, 2001]. Weddell seals exploit habitat depending of the local sea ice conditions [Heerah et al., 2016]. For example, in regions with variable sea ice (e.g. Davis), seals hunted longer in more concentrated sea ice compared with areas where sea ice conditions were persistent and less variable (e.g. Dumont d'Urville), where seals hunted longer in less concentrated sea ice. **As for SESs, there is a compromise between feeding within sea ice and being imped by it. Surprisingly, polynyas were not important features for Weddell seals unlike male SESs.** Weddell seals are ice-obligate species with the ability to break ice, and they required ice thick enough to ensure platform for haulout and thin enough to allow seals to maintain breathing holes [Lake et al., 2005]. They are known to interact with smaller features such as perennial tide cracks [Kooyman, 1981]. **The main difference between SESs and Weddell seal foraging strategies within sea ice seems to be the spatial range of their foraging activity.** For Weddell seals, the foraging activity is concentrated within 5 km of a breathing hole, and they appear to move between holes as local food is depleted [Heerah et al., 2016]. **In contrast SESs undertake large migration from their subantarctic breeding colonies, and although some individuals remained in the same polynyas for the whole winter, some others, travelled long distances within the Antarctic continental shelf, from one polynya to another, or switched from the shelf break to the coast before returning to the colony. In terms of hydrological properties, similarly to male SESs using the AASW/mCDW in the ASC, Heerah et al. [Heerah et al., 2013] demonstrated that Weddell seals at Dumont D'Urville mainly used the mCDW over complex bathymetry on the shelf.** Lacarra et al. [Lacarra et al., 2011] suggested a flow of this nutrient-rich water mass from the d'Urville Trough to the coastal zones likely stimulating primary and secondary production.

9.4 Emperor penguins

Emperor penguins forage under winter sea ice at two key periods and adopt different foraging strategies for each: after egg-laying, between autumn and mid-winter when females are rebuilding their reserves (while the males incubate eggs); and during the chick provisioning period from mid-winter to December when both males and females alternate periods of foraging. From autumn to spring, emperor penguins in East Antarctica forage either in polynyas over the continental slope (the slope polynya), or in pack-ice regions further off-shore [Kirkwood and Robertson, 1997a, Kirkwood and Robertson, 1997b]. The slope polynyas was thought to be the prime foraging habitat because of the higher abundance of Antarctic krill, Antarctic silverfish and glacial squid in the vicinity of the slope (dominating the penguin's diet) and providing the closest open water area to the colonies. **This emphasizes the important role of polynyas in the winter for predators allowing them to forage within productive regions such the continental slope by providing open water ac-**

cess. Females presumably feed on krill and Antarctic silverfish between late May and early August [Kirkwood and Robertson, 1997b]. Then, both sexes may forage on krill in August diving to depths below 100 m (as krill presumably remains at depth during the day, see Figure I.11) while during September and October, they performed shallower dives to depths < 100 m likely due to the increased of squid in their diet [Kirkwood and Robertson, 1997a]. **This provides insight into the potential prey encountered by male SESs at shallow depths in winter coastal polynyas. It may also explain why SES maximal depths decreased in polynyas from August to October (see Figure V.9), likely following prey distribution.**

10 Limits and perspectives

In this thesis, I attempted to provide new insights into the foraging ecology of a non-sea ice obligate mesopredator within winter sea ice. However, there were several analytical considerations that may influence the conclusions. These include:

- The interpretation of the foraging index based on different assumptions;
- The lack of information on SESs diet in the Antarctic sea ice zone;
- The absence of broader oceanographic context due to the only use of hydrological data collected *in situ* during the seal dives, preventing quantification and contrast of habitat used and not used by;
- The interpretation of the satellite sea ice data in some regions. For example, the presence of thin ice early in the season or multi-year sea ice in polynyas may lead to artefacts in the estimation of sea ice concentration (see chapter IV);
- The still lack of information about sea ice thickness, which could provide invaluable information on the biological communities supported by sea ice;
- The considerable lack of knowledge about the under ice Antarctic ecosystems in winter.

Here, I review three major limits and the implications for my biological interpretation. These are (i) the interpretation of the foraging metric for low resolution dive data, (ii) the lack of information on SES diet during their winter trip, and (iii) the current lacking knowledge on the under ice ecosystems in winter.

10.1 Interpretation of the foraging metric

As highlighted by Heerah et al. [Heerah, 2014], intensification of the foraging effort is likely to occur several times within a dive and not necessarily only during the bottom phase. When only dive data are available, hunting time, the total time within a dive comprised

of segments of decreased velocity, is a straightforward way to estimate the time spent foraging during the whole dive [Heerah, 2014, Heerah et al., 2015]. We also used the predicted prey encounter events (PEE; derived from combined maximum depth, bottom time, ascent and horizontal speed for pelagic strategy or dive duration and ascent speed for demersal strategy, see chapter II) in an attempt to use PEE derived information when PEE were not available (see Chapter II). Although we did not quantify the similarities and differences between the two metrics, they seemed to be generally in good agreement in the chapter V.

However two competing views exist on how marine predators modify their diving behaviour in different environments, and on the signification of increased time spent at a given depth. The first focuses on the animal's physiology in relation to oxygen stores and suggests that increased dive duration generally indicates increased prey density and foraging success [Austin et al., 2006]. The second considers prey quality and distribution, and suggests that longer dive durations are due to lower prey densities and foraging success; seals foraging in high-quality patches are likely to have a high prey-capture rates and therefore terminate dives sooner [Charnov, 1976]. Dive duration or bottom time are commonly used as a proxy of foraging and prey acquisition following one of the two views. However, recent findings suggest the situation is not this simple [Dragon et al., 2012a, Gallon et al., 2013, Thums et al., 2013, Bestley et al., 2015, Jouma'a et al., 2016]. Dive physiological limits may reduce the opportunity to hunt during deeper dives compared with shallow dives [Thompson and Fedak, 2001] and there is no simple way to take this into account. A recent work by Jouma'a et al. [Jouma'a et al., 2016] on high resolution dive data of SESs investigated the link between bottom duration and PEE derived from accelerometers. Four findings are interesting for our discussion:

- 1. Unsuccessful dives with no PEE have a longer bottom time than successful dives, in accordance with findings by Thums et al. [Thums et al., 2013], but represented only 10% dives of SES dives;
- 2. Beyond 550 m dive depth, bottom time starts decreasing with increasing dive depth regardless whether or not the dive was successful and unsuccessful (presence or absence of PEE);
- 3. For 90% of dives (successful dives, with at least one PEE), bottom time increased with the number of PEE at depth greater than 250 m;
- 4. About 73% of PEE occurred during the bottom phase, while 27% occurred during the descent/ascent phase.

Therefore, for 90% of dives, the bottom time is a good indicator of foraging success. Hunting time encompasses foraging effort both at the bottom and transit phase and is well correlated with bottom time. The validity of hunting time is thus dependent on diving depth, and below 550 m it may be biased as shorter bottom times (reflecting the physiological dive limits) may be associated with good foraging success. However we found that

the average dive depth of seals foraging within the sea ice region was around 400 m, so this bias may only concern deep dives within canyon along the Antarctic shelf or along the shelf break. Moreover, hunting time segments were associated with a large proportion of PEE (68% of all PEE inferred from acceleration data) and with four times more PEE than other segments [Heerah, 2014, Heerah et al., 2015]. We are thus confident that this index is reliable for evaluating foraging activity of SESs within the sea ice region.

Among all available SES foraging indices (except body condition), none take into account the quality and size of the prey. Small, schooling prey may lead to higher PEE rate but to longer or shorter hunting time depending on the behaviour of the prey (e.g. pursuit of a single prey, or feeding within schools without moving), while larger prey may lead to fewer PEE, but to variable hunting times depending on the behaviour of the prey and the time required to handle it. Moreover, long and costly dives might be used to capture highly rewarding prey. Finally, for ice-associated species, sea ice might also alter the dive structure, for example by constraining the dive to within an area surrounding an open access point to air. This would result in short dives without any increased foraging success. Sea ice can also alter the dive structure by aggregating preys beneath the ice. It is therefore likely that foraging strategies are changeable among dives, zones and individuals [Bestley et al., 2015].

To conclude, the relationship between dive duration and patch quality is complex and depends on several factors such as prey size, energy content, distribution. However, for some questions, such as this thesis, where a species has a reasonably stable diet and stable habitat use, relative changes in hunting time and dive behaviour (i.e. PEE) still provide very valuable insights.

Considerable effort should be made to deploy accelerometers over the long winter trips of land based species such as post-moult elephant seals. As detailed in section 6.3.1, these new sensors enable the estimation of energy expenditure and intake. Finally, the time-series of descent vertical speed on low resolution dive data may be promising in describing the change in body condition and will be used to complete the chapter V.

10.2 Southern elephant seal diet

The absence of information on SES diet in the Antarctic zone underpins speculation in the interpretation of the different foraging strategies. The combined use of the three methods detailed below or one of these can provide information to combine with dive and tracking analysis:

- Analysis of blood samples using stable isotope analysis provides information about the prey's geographical origin with carbon ($\delta^{13}C \sim {}^{13}C / {}^{12}C$) and trophic position of a consumer with nitrogen ($\delta^{15}N \sim {}^{15}N / {}^{14}N$) over the last 2-3 months which is largely the return phase of a SES winter trip [Bailleul et al., 2010a, Authier et al., 2012b];

- Analysis of blubber samples using fatty acid analysis can provide longer-term history of diet [Bradshaw et al., 2003, Newland et al., 2009, Banks et al., 2014], more informative on their time within sea;

- Analysis of whiskers using stable isotope analysis provide information about the diet's geographical origin with carbon ($\delta^{13}C \sim {}^{13}C / {}^{12}C$) and trophic position of a consumer with nitrogen ($\delta^{15}N \sim {}^{15}N / {}^{14}N$) as detailed previously but over longer time scale corresponding to the last 12 to 24 months [Newland et al., 2011, Hückstädt et al., 2012, Walters et al., 2014, Beltran et al., 2015]. However, it can be difficult to relate the time-series of stable isotope ratios of carbon and nitrogen contained in whiskers to individual telemetry tracks due to the haphazard way seals moult and replace their whiskers. It requires knowledge of the growth history of the whisker [Walters et al., 2014].

10.3 Under ice ecosystems: a "blind spot"

This thesis has had only limited ability to describe mechanisms between sea ice and the biotic components of the underlying Antarctic ecosystems due to the limited knowledge of the under ice particularly during the winter season. This issue was developed in the discussion of each chapter and highlighted in the general introduction (I). Briefly, information needed during the winter season is:

- The primary production within sea ice and its timing. This is still limited by sporadic information due to limited ship access, and non-detection of ice-associated phytoplankton in conventional satellite ocean-colour images [Fritsen et al., 1994, Lieser et al., 2015];

- The zooplankton at the ice-ocean interface, dominated by Antarctic krill and crystal krill. Considerable efforts are made to improve the knowledge of the seasonal distribution and the reliance of Antarctic krill to Antarctic sea ice [Flores et al., 2012b, Flores et al., 2012a, Schaafsma et al., 2016]; however, significant efforts should be made to understand also its obligate ice form, crystal krill;

- Ichthyoplancton and macrofauna at the ice-ocean interface up to mesopelagic depths. Little is known about their vertical and horizontal distribution in winter and how sea ice conditions influence their life cycle (e.g. reviews [Koz, 1995, Barrera-Oro, 2002, Koubbi et al., 2009]; summer surveys [Fuiman et al., 2002, La Mesa et al., 2010, Koubbi et al., 2011, Ashford et al., 2012]; late summer/autumn surveys [Hoddell et al., 2000, Lancraft et al., 2004, Van de Putte et al., 2010]; winter surveys [Flores et al., 2008, Flores et al., 2011, David et al., 2016]);

- Which species are caught by upper trophic levels and at which depths within the winter sea ice; this is impeded by the two previous points, i.e. our knowledge of the species present in winter and their distribution on the water column, and this is associated with the second limit of this study regarding the lack of information on SES diet in winter.

Ships-based acoustic surveys and net sampling could considerably increase our knowledge of under ice ecosystems, but extreme weather and sea ice conditions still do not allow ship to visit these areas during winter. However, station-based deployments of autonomous underwater vehicles for imaging and acoustic surveys beneath sea ice could considerably fill this gap in winter. Moreover, simple moorings could be deployed within sea ice or could also be deployed in winter close to Antarctic station. Recording images at the sea ice interface or along a cable on the Antarctic shelf or at mesopelagic depths within the pack ice region could also provide significant information on the trophic linkages beneath sea ice in winter.

11 Concluding thoughts

I would like to finish this manuscript by some important considerations that came up to me and that I matured while putting my results together over these last three years. Both investigating the role of the spatio-temporal variability of sea-ice on seal foraging behavior (chapter III), or proposing mechanisms by which climate forcing affects biotic and abiotic components of the Antarctic marine ecosystem (chapter IV) remain very challenging, and implied pushing our observations to their limit. I personally give much importance of pushing observation to their limit to extract the very last drop of relevant information in them, but that needs to come with some hindsight, which I would like to develop here.

One important challenge of ecology (and more generally of science), is to develop an understanding of complex systems, by seeking simple patterns and through this, developing the ability to make predictions without compromising its complexity [Begon et al., 2006]. In this thesis, I tried to address this by developing and proposing simple hypotheses of complex ecological linkages, providing a step towards answering some complex environmental questions. This required balancing an alternative point of view; that (over) simplification of complex processes may lead to misinterpretations of ecological mechanisms. This might be especially true for the Antarctic sea ice ecosystem, which is driven by multiple processes at a wide range of scales. High individual variability, expressed for instance by plastic foraging strategies, the role of learning or experience may hamper disentangling the complexity. Finding simple linkages between sea ice conditions and upper trophic levels is therefore extremely challenging. I tackled this challenge by establishing simple linkages within a well-established mechanistic framework: linkages from climate variability to sea-ice; from sea-ice to oceanographic conditions and lower trophic levels; from lower to upper trophic levels. Therefore trying to reduce the complexity of the

problem at the level of each of these linkages, supported by mechanistic understanding; instead of looking for high amount of variance explained between simplified environmental and foraging indexes. As part of the last three years, I challenge my research with such strategy, in an attempt to understand the complex and fascinating processes I studied, but also limited myself to push observations too far and drop into oversimplifications.

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APPENDIX A

General information on deployment for training and study dataset

Table AX1: General information of the 36 post-breeding SES females (training dataset) including deployment date, animal weight and snout-to-tail length upon deployment, tag type deployed, number of dives, trip duration, mean number of dives per day, and mean distance travelled per day between the first and last locations of each day. Mean are expressed ±SD.

ID	Deployment	Weight (kg)	Length (cm)	Splash-10-F	TDR-MK10-X	Argos-CTD	SPOT	Nb. dives	Trip (d)	Dives/day	Dist./day (km)
2010-18	26/10/2010	352.5	246	X	X			3361	60	551 ± 4.5	54.2 ± 24.9
2010-19	31/10/2010	NA	266	X	X			4123	73	55.7 ± 8.6	53.7 ± 36.5
2010-21	18/11/2010	425	278	X	X			4519	73	61.1 ± 7.6	65.4 ± 23.8
2011-14	25/10/2011	252	240		X	X		994	11	82.8 ± 25.8	68.9 ± 32.2
2011-16	26/10/2011	255	254	X	X			653	10	59.4 ± 9.9	67.4 ± 26.8
2011-17	26/10/2011	225	225		X	X		809	10	73.5 ± 11.2	15.2 ± 15.5
2011-18	26/10/2011	245	238	X	X			1030	12	79.2 ± 10.6	87.0 ± 22.1
2011-21	28/10/2011	245	225	X	X			3768	53	69.8 ± 7.3	34.5 ± 23.8
2011-26	30/10/2011	255	232	X	X			3727	57	63.2 ± 11.1	36.1 ± 22.9
2011-27	30/10/2011	236	235	X	X			1229	14	81.9 ± 18	74.9 ± 20.9
2011-28	30/10/2011	249	240	X	X			3707	55	65.0 ± 11.9	46.1 ± 19.5
2012-1	27/10/2012	230	232	X	X			1867	23	77.8 ± 12.5	54.9 ± 21.9
2012-2	27/10/2012	362	235	X	X			1135	20	54.0 ± 6.5	76.2 ± 14.6
2012-3	27/10/2012	300	261	X	X			1710	22	71.3 ± 16.5	40.9 ± 34.7
2012-4	27/10/2012	282	248	X	X			1532	23	63.8 ± 11.6	53.4 ± 23.5
2012-6	28/10/2012	330	235	X	X			1495	22	65 ± 8.5	71.3 ± 24.2
2012-9	02/11/2012	328	247	X	X			1476	22	67.1 ± 7.0	68.2 ± 21.3
2012-11	01/11/2012	333	247		X	X		1570	23	65.4 ± 5.9	45.6 ± 21.3
2012-14	01/11/2012	258	229		X	X		2045	28	70.5 ± 15.0	14.7 ± 13.3
2012-15	01/11/2012	275	235		X	X		1664	23	72.3 ± 4.9	28.7 ± 13.6
2012-16	01/11/2012	425	265		X	X		1385	25	53.3± 8.9	8.0 ± 6.8
2012-17	01/11/2012	288	251		X	X		1620	24	64.8 ± 3.7	24.2 ± 14.8
2012-18	02/11/2012	328	252		X	X		1735	25	66.7 ± 7.0	3.0 ± 2.7
2013-1	28/10/2013	269	250	X	X			1724	26	63.9 ± 12.1	52.5 ± 20.1
2013-2	28/10/2013	240	220	X	X			1964	25	75.5 ± 11.2	56.6 ± 30.9
2013-3	29/10/2013	286	240	X	X			1583	23	66.0 ± 4.5	53.3 ± 21.5
2013-4	29/10/2013	268	235	X	X			1256	18	66.1 ± 11.6	72.9 ± 22.1
2013-5	29/10/2013	296	247	X	X			1262	17	70.1 ± 10.2	26.4 ± 16.8
2013-6	29/10/2013	250	236	X	X			1284	16	71.3 ± 20.0	74.1 ± 26.6
2013-7	30/10/2013	331	260	X	X			1816	26	67.3 ± 7.0	52.9 ± 14.9
2013-10	30/10/2013	300	245		X	X		1955	29	65.2 ± 7.3	56.2 ± 28.3
2013-11	30/10/2013	277	240		X	X		2025	27	72.3 ± 14.9	68.6 ± 21.4
2013-12	31/10/2013	279	230		X	X		1686	23	70.3 ± 10.3	50.6 ± 40.0
2013-13	31/10/2013	264	240		X	X		1742	24	72.6 ± 5.2	53.6 ± 26.9
2013-16	02/11/2013	236	225		X		X	1802	23	75.1 ± 12.0	60.5 ± 28.4
2013-18	02/11/2013	293	245		X		X	1595	25	63.8 ± 3.1	42.2± 20.3
Mean ± SD		**287.5 ± 50.5**	**243.2 ± 13.7**					**1952 ± 972**	**29 ± 17**	**65.2 ± 12.1**	**49.8 ± 30.1**

Table AX2: General information of the 35 post-moulting SES (study dataset) including sex, deployment date, animal weight and snout-to-tail length upon deployment, number of dives, trip duration, mean number of dives per day, and mean distance travelled per day between the first and last locations of each day. Additional information on CTD profiles is also included such as the mean number of CTD profiles per day, the total CTD profiles, mean of points per CTD profiles, the mean time interval between dive and CTD profile associated and the mean distance between dive and CTD profile associated. Mean are expressed ± SD.

ID	Sex	Deployment	Weight (kg)	Length (cm)	Nb. dives	Trip (d)	Dives per day	Dist. per day (km)	CTD profiles per day	Nb. CTD profiles	Points per CTD profile	Time dive-CTD (min)	Dist. dive-CTD (km)
2004-1	M	02/27/2004	368	250	553	25	25.1 ± 12.1	79.8 ± 44.9	X	X	X	X	X
2004-2	M	02/27/2004	385.5	267	6133	133	45.7 ± 20.1	39 ± 34.6	2.9 ± 1	336	9 ± 1.5	287.6 ± 189.3	9.1 ± 9.5
2004-3	F	02/21/2004	297.5	233	5363	140	38 ± 20	35.8 ± 30.4	2.6 ± 1.1	299	9.5 ± 1.3	289.8 ± 183.9	11.5 ± 10.5
2004-5	M	02/25/2004	469.5	282	7209	163	45.6 ± 18.1	26 ± 32.1	2.7 ± 1	371	8.9 ± 1.5	284.3 ± 184.3	7.5 ± 9
2004-6	F	02/22/2004	347	240	4248	167	27.4 ± 12.3	29.2 ± 26.2	2.5 ± 1	96	9 ± 1.5	274.5 ± 175.1	11.6 ± 9.7
2004-7	F	02/22/2004	295.5	238	6021	155	39.9 ± 18.8	43.8 ± 28	2.2 ± 1	300	9.4 ± 1.4	293.8 ± 189.7	13.4 ± 10.4
2004-8	M	02/24/2004	274	235	7530	163	50.2 ± 25.3	43.1 ± 34	2.5 ± 1.1	343	8.9 ± 1.4	241.9 ± 173.3	10.3 ± 10.7
2004-10	F	02/21/2004	363.5	258	7503	161	46.3 ± 23.6	36.1 ± 30.6	2.7 ± 1	324	9.3 ± 1.3	267.2 ± 177.1	9.6 ± 9.4
2008-1	M	21/12/2007	266	230	8815	252	39.3 ± 30.4	35.7 ± 27.4	X	X	X	X	X
2008-2	F	22/12/2007	169	200	6031	155	38.9 ± 16.2	46.8 ± 30.4	X	X	X	X	X
2008-6	F	22/01/2008	290	242	6200	205	31 ± 10.3	45.9 ± 27.6	X	X	X	X	X
2008-7	F	26/01/2008	377	267	5253	166	32.2 ± 12.5	45.1 ± 31.6	1.7 ± 0.5	275	23.7 ± 6.2	297.4 ± 186.4	11.8 ± 10.8
2009-16	M	01/01/2009	258	249	5887	153	39.7 ± 18	35.9 ± 28.8	1.9 ± 0.3	266	25.7 ± 4	255.6 ± 157.6	9 ± 8.7
2011-1	M	24/01/2011	680	316	1002	24	40 ± 13	101.7 ± 25.9	1.8 ± 0.4	42	26.1 ± 3.7	238.6 ± 153.1	18.6 ± 12.5
2011-4	M	21/01/2011	800	330	4438	105	41.8 ± 11	34.1 ± 39.5	1.9 ± 0.4	411	26.5 ± 2.2	271.1 ± 173.6	8.8 ± 10
2011-6	F	12/02/2011	284.6	233	4230	86	50.3 ± 11.3	35.8 ± 31	2 ± 0.2	432	26.7 ± 1.8	237.6 ± 161.5	12 ± 10.1
2011-7	M	21/01/2011	452.5	280	4749	79	59.4 ± 18.8	41 ± 40.8	1.7 ± 0.5	104	26.7 ± 1.3	296.9 ± 187.6	13.5 ± 10.8
2011-9	M	22/01/2011	628.5	326	3487	110	31.7 ± 12	31.4 ± 38.2	1.8 ± 0.4	407	25.2 ± 4.4	295.3 ± 185.2	10.4 ± 11.6
2011-10	F	26/01/2011	330	250	3041	81	37.1 ± 11.4	36.3 ± 27.1	X	X	X	X	X
2012-1	M	21/01/2012	523	291	9799	235	42.4 ± 17.6	35.1 ± 28.4	3.2 ± 0.8	737	15.8 ± 2.8	192.4 ± 152.8	8.9 ± 9
2012-3	M	21/01/2012	454	277	4297	94	45.2 ± 10.8	37.9 ± 38.8	3.4 ± 0.8	321	16.1 ± 2.5	239.1 ± 171.1	8 ± 8
2012-2	F	05/02/2012	303	233	7178	233	30.9 ± 12.4	30.7 ± 21.3	X	X	X	X	X
2013-1	F	24/02/2013	340	262	8079	234	34.4 ± 9.2	46.7 ± 31.6	3.1 ± 0.8	718	14.8 ± 2.9	195.3 ± 151.7	7.7 ± 8.1
2013-2	M	28/02/2013	1100	370	8321	239	39.3 ± 17.4	40.3 ± 44.7	3.3 ± 0.8	627	15.3 ± 2.2	237.5 ± 178.2	7.7 ± 9.1
2013-3	M	10/02/2013	468	280	1513	35	45.8 ± 9.4	78.5 ± 31.2	3.2 ± 0.8	105	14.9 ± 2.7	179.3 ± 142.2	12.1 ± 10.5
2013-4	M	27/02/2013	850	333	6064	190	34.9 ± 12.3	40.2 ± 38.4	3 ± 1	560	14.8 ± 2.9	199.3 ± 159.7	7.1 ± 8.4
2013-5	F	07/02/2013	336	254	11732	296	43.4 ± 16.4	37.2 ± 28.7	3.1 ± 0.9	702	14.9 ± 2.7	189.2 ± 159.4	7.2 ± 8.4
2013-7	F	17/02/2013	410	248	9204	239	41.7 ± 13.8	47.1 ± 34.8	3.1 ± 0.9	707	15.1 ± 2.4	189.2 ± 153.9	7.2 ± 7.9
2013-9	M	11/02/2013	470	300	1517	31	47.4 ± 14.8	73.7 ± 45.2	3.5 ± 0.6	111	15.2 ± 2.4	163.9 ± 137.6	10.2 ± 11.2
2013-11	M	10/02/2013	556	256	10151	238	43.9 ± 13.3	25.3 ± 35.1	3.2 ± 0.8	730	15 ± 2.6	214.5 ± 165.6	5.3 ± 6.9
2013-12	M	12/03/2013	1150	375	7728	232	36 ± 11.9	35 ± 19.8	3 ± 0.9	657	14.7 ± 2.8	204.3 ± 163.7	6.3 ± 6.5
2013-13	M	10/02/2013	600	321	3501	69	50 ± 17.4	54.9 ± 36.2	3.4 ± 0.8	220	15.6 ± 1.7	170.9 ± 139.3	8.8 ± 9.3
2013-14	M	17/03/2013	300	270	10074	252	42.2 ± 16	22.3 ± 35.7	3.2 ± 0.8	660	15.1 ± 2.5	216.3 ± 167.7	3.8 ± 5.9
2013-15	F	10/02/2013	366	248	8335	231	37.9 ± 9	50.6 ± 25.6	3.3 ± 0.7	733	15.1 ± 2.5	173.6 ± 137.7	7.4 ± 7.4
2013-18	F	07/02/2013	346	255	6723	177	41.3 ± 14.6	36.7 ± 30.4	3.1 ± 0.9	510	14.8 ± 2.7	190.4 ± 144.7	6.7 ± 6.9
Mean ± SD			**454.5 ± 226.1**	**271.4 ± 40.5**	**6054 ± 2742**	**159 ± 75**	**40.1 ± 17.5**	**38.7 ± 33.2**	**2.8 ± 1**	**417 ± 225**	**15.8 ± 5.6**	**225 ± 169**	**9.1 ± 9.6**

Criteria to identify demersal and pelagic dive strategies

Training dataset

For each seal, beginning and end of tracks were removed (60 first and last dives) as they arguably correspond to intermediate dives not associated with a particular strategy, and could therefore bias predictive models. In order to separate pelagic dives from demersal dives, for each dive the difference between the bathymetry (based on GEBCO gridded bathymetry data of 30' resolution; H_{GEBCO}) at the corrected dive position, and the mean averaged depth at the bottom phase of the dive (H_{DIVE}) was computed. Depth difference histogram (i.e. H_{GEBCO}-H_{DIVE} ; Figure AX1A) showed several mode at a number of depth (around 0 m; around 100 m; around 1500 m; around 3200 m; 4000 m and around 5000 m). Arguably the demersal dives are all dives close to the bottom; i.e. within the first mode, close to H_{GEBCO}-H_{DIVE} = 0. We therefore chose the separation of the two first modes (around 0 m and around 100 m) as the separation for demersal and pelagic dives. These two first mode are separated by a low trough in the distribution at H_{GEBCO}-H_{DIVE} = 80 m. Consequently, we define the demersal dives with a depth difference H_{GEBCO}-$H_{DIVE} \leq$ 80m. We note that in an ideal case, demersal dives should all be associated to H_{GEBCO}-H_{DIVE} close to 0, however we consider that the spread of the mode associated to demersal dives (i.e. the mode corresponding to H_{GEBCO}-$H_{DIVE} \leq$ 80m) results from errors in bathymetry and/or errors in location. Among those, we found that 1.7% of dives had an averaged dive depth greater than bathymetry at the same position. Those dives were kept and also included into demersal dives.

For 2 individuals we found that the two lowest modes in the distribution of H_{GEBCO}-H_{DIVE} were not associated to 0 and 100 m but with 50 and 150 m (Figure AX1B). Looking more closely at these two individuals, we actually found that the diving profiles were actually following the underlying bathymetry depth with a given offset, suggesting that the two individuals were actually performing demersal dives while depth difference were higher than 80 m. The depth difference for these two individuals was then corrected due to hypothetic error in bathymetry and their dives were defined as demersal.

All other dives with a depth difference > 80m were classified as pelagic dives. For days where both strategies were present, the strategy retained was the dominant one (with the higher number of dives). Finally, only days with more than 15 dives performed into one of the two strategies and a minimum of 2 days spent over the Kerguelen shelf were kept. From 36 individuals, all were exhibiting a pelagic dive strategy and 8 were exhibiting both demersal and pelagic strategies.

Study dataset

9.3% of dives were deeper than the bathymetry at the same position. All positions with a maximum dive depth greater than the bathymetry (Figure AX2) were clearly located in the Antarctic shelf break zone, so those dives were included into the demersal group and bathymetry value was corrected at each position by the value of the maximal depth of the dive. Similar than for the training dataset, the depth difference histogram (H_{GEBCO}-H_{DIVE}; Figure AX1C) was distributed with a number of modes (around 0 m; 3300 m; 4000 m; and 5000 m). But conversely to the training dataset, the mode around 0 m is not clearly sep-

arated with another closely spaced mode, making the separation between demersal versus pelagic dives less clear than for the training dataset. We note however, that the mode around 0 m rapidly drops when reaching depth difference around 160 m. We therefore defined the demersal dives as all dives with a difference histogram H_{GEBCO}-$H_{DIVE} \leq 160$ m. Dives with a depth difference > 160 m were defined as pelagic. Deep dives in canyons on the shelf were classified demersal due to possible interaction with topography along canyons. Finally, for days where both strategies were present, the strategy retained was the dominant one (with the higher number of dives). All 35 individuals were exhibiting a pelagic dive strategy, of which 25 also used a demersal strategy during part of the trip.

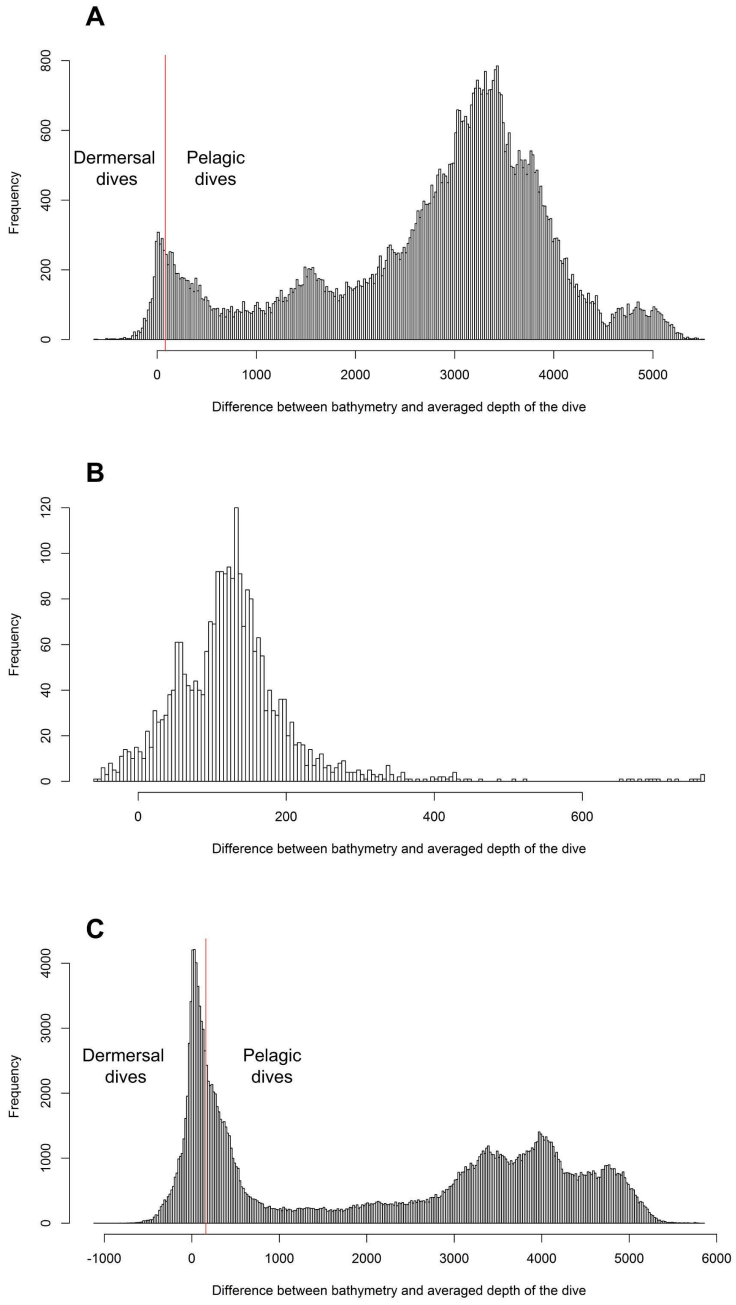


Figure AX1: Histograms of the depth difference (m) between the bathymetry at the corrected dive position and the mean averaged depth of the animal for A) 34 post-breeding female SES of the training dataset and B) 2 post-breeding female SES of the training dataset for which the threshold to identify demersal/pelagic dives was modified with depth difference higher than 80 m while they exhibited mostly demersal dives, C) 35 post-moulting female SES of the study dataset. The red line represents the threshold to identify demersal dives and pelagic ones, set at 80 m (a) and 160 m (c).

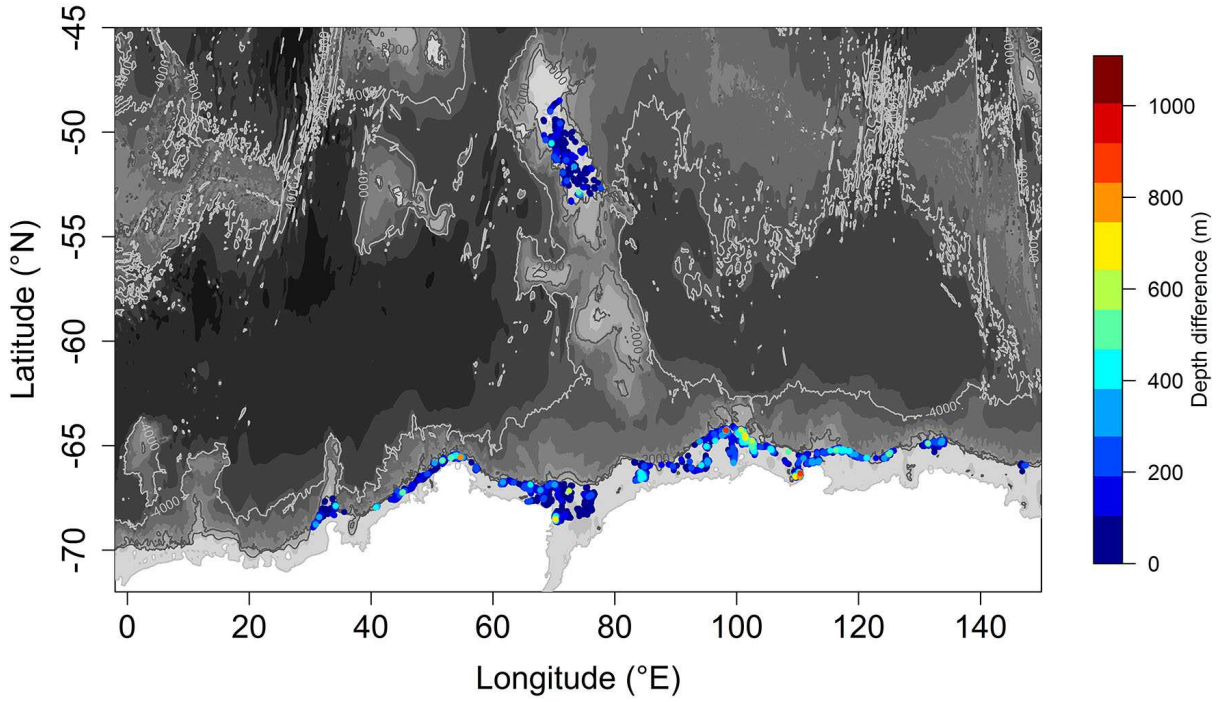


Figure AX2: Positions of the dives deeper than the bathymetry for the 35 post-moulting animals equipped from 2004-2013 (study dataset).The scale is the difference between the bottom depth of the dive and the local bathymetry.

The statistical model

GLMM for foraging behaviour

A generalized linear mixed effects model was fitted for each strategy with a quasi-poisson distribution to take into account both under- and overdispersion. Individuals were included as a random intercept. The R package *MASS* (from R Development Core Team, 2009) with the function *glmmPQL* using multiplicative dispersion and penalized quasilikelihood was used. Outliers and homogeneity in the variables were checked following steps described in [Zuur et al., 2010]. Collinearity (coef. > 0.5) was tested between variables using Pearson correlation [Zuur et al., 2010] and one of each highly correlated pair were removed. Explanatory variables of training and study datasets were standardized (centered and scaled, combining both datasets) to facilitate model convergence and to be able to compare the respective contribution of the predictors. One full model for each strategy was first computed, then a marginal R-squared (i.e. variance explained by fixed factors only) and a conditional R-Squared (i.e. variance explained by both fixed and random factors) were calculated as described in [Nakagawa and Schielzeth, 2010, Nakagawa and Schielzeth, 2013].

Model validations were checked by plotting Pearson and response residuals against fitted values, and against each explanatory variable, verifying homogeneity and normality of residuals [Zuur et al., 2010].

The predictive ability of each model applied to a particular data set was estimated using leave-one-out cross-validation (thereafter "CV process"; e.g. see [Harrell, 2001]. For each data set, the following steps were repeated for each individual:

- a) the dataset was first divided into a training subset consisting of all individuals minus one and a validation subset consisting of the remaining animal;
- b) a predictive model was then built based on the training data; using *glmmPQL*, model selection can only be performed according to p-values, a stepwise procedure was implemented with a threshold set at p = 0.05 and only significant variables were retained for the predictive model;
- c) the model obtained in step b (regression coefficients) was applied to the validation subset to predict responses;
- d) the cross-validation mean squared prediction error was finally computed following [Murtaugh, 2009];
- e) this procedure was repeated for all individuals. After the CV process, MSPE computed for each individual allowed us to describe the predictive ability of the training dataset on each individual. In parallel, the deviance explained by the two models was calculated using prediction of the cross-validation. Finally, to avoid model overfitting the training dataset, regression coefficients computed at each step of the cross-validation were averaged to obtain coefficients that was then applied for the prediction on the study dataset.

GLMM for habitat

To take into account important over dispersion, GLMMs with a negative binomial distribution with Laplace approximation [Bolker et al., 2009] were fitted using the package *glmmADMB* and the function *glmmadmb* in R software [Fournier et al., 2012]. Individuals were included as a random intercept. Outliers, homogeneity and collinearity were checked similarly to the section "GLMM for foraging behaviour". Explanatory variables were standardized. Model selection was made using the likelihood ratio test, starting from a full model with fixed effects retained only if they improved the fit ($p < 0.05$, [Zuur et al., 2010]). It was then checked that the most parsimonious model was also the model with the lowest Akaike's Information Criteria (AIC). The optimal model was then fitted and residuals were plotted to verify their homogeneity and validate models ([Zuur et al., 2010]).

Visualization of demersal and pelagic dive strategies for the study dataset

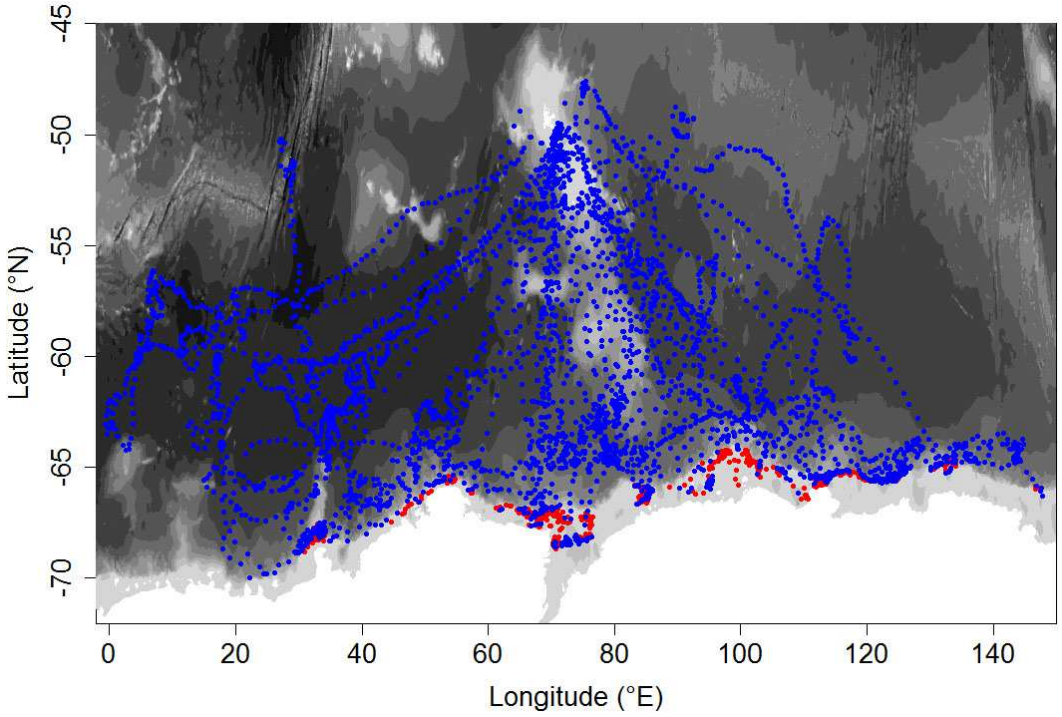


Figure AX3: Tracks of the 35 post-moulting animals equipped from 2004 to 2013 associated with their dive strategies. In red is presented the demersal dive strategy while in blue the pelagic dive strategy.

APPENDIX B

Table BX1: General information of the 46 post-moulting SESs including sex, dive start and end date, date of return when the tag did not stopped (and direction when they headed at-sea again South or East), number of Argos position transmitted daily, animal weight and snout-to-tail length upon deployment, total number of dives, mean number of dives per day and mean distance travelled per day between the first and last locations of each day. Additional information on behaviour towards sea ice is also included such as animals visiting the sea ice region, their maximal distance from the sea ice edge, the percentage of shallow dives (i.e. less or equal to 40m) performed under sea ice and their hunting time per dive. Negative distances refer to distances into the pack from the ice edge, and positive distances refer to distances north of the ice edge. Mean are expressed ± SD.

ID	Sex	Start date	End date	Date of re-turn	Nb. of location per day	Weight (kg)	Length (cm)	Total dives	Nb. dives per day	Dist. per day (km)	Visit sea ice	Max dist. to sea ice (km)	Shallow dives in sea ice (%)	Hunting time per dive in sea ice (min)
2004_1	M	04/03/2004	29/03/2004		8 ± 4	368	250	553	25 ± 12	75 ± 49	×	-62	12%	5.4 ± 3.9
2004_2	M	27/02/2004	09/07/2004		18 ± 7	385.5	267	6133	46 ± 20	34 ± 33	×	-192	7%	11.3 ± 7.3
2004_3	F	01/03/2004	19/07/2004		14 ± 9	297.5	233	5363	38 ± 20	34 ± 29	×	-345	1%	14.6 ± 11.3
2004_5	M	25/02/2004	06/08/2004		17 ± 6	469.5	282	7209	46 ± 18	22 ± 31	×	-341	10%	14 ± 10
2004_6	F	22/02/2004	07/08/2004		12 ± 6	347	240	4248	27 ± 12	28 ± 26	×	-165	1%	22 ± 10.2
2004_7	F	29/02/2004	02/08/2004		15 ± 9	295.5	238	6021	40 ± 19	42 ± 28	×	-110	2%	8.5 ± 4
2004_8	M	27/02/2004	08/08/2004	6 (S)	17 ± 9	274	235	7530	50 ± 25	40 ± 34	×	-610	6%	5.4 ± 4.7
2004_10	F	29/02/2004	08/08/2004		16 ± 10	363.5	258	7503	46 ± 24	31 ± 29	×	-367	5%	13 ± 10
2008_1	M	01/01/2008	08/09/2008		9 ± 5	266	230	8815	39 ± 30	33 ± 26	×	-161	8%	10 ± 7.5
2008_2	F	24/12/2007	27/05/2008		14 ± 7	169	200	6031	39 ± 16	44 ± 30		-8		
2008_6	F	24/01/2008	16/08/2008		11 ± 4	290	242	6200	31 ± 10	42 ± 26	×	-3	0%	11.3 ± 6.2
2008_7	F	27/01/2008	11/07/2008		15 ± 7	377	267	5253	32 ± 13	44 ± 32	×	-244	1%	17 ± 9.8
2009_16	M	01/01/2009	03/06/2009	6	17 ± 7	258	249	5887	40 ± 18	34 ± 28	×	-155	4%	9.4 ± 7
2011_1	M	27/01/2011	20/02/2011		21 ± 7	680	316	1002	40 ± 13	98 ± 30		50		
2011_4	M	31/01/2011	16/05/2011		26 ± 7	800	330	4438	42 ± 11	33 ± 39	×	-316	2%	13.5 ± 7.1
2011_6	F	19/02/2011	16/05/2011		31 ± 9	284.6	233	4230	50 ± 11	32 ± 31	×	-4	0%	10.6 ± 5.8
2011_7	M	26/01/2011	15/04/2011		34 ± 10	452.5	280	4749	60 ± 19	36 ± 39	×	-302	14%	9.3 ± 6.5
2011_9	M	27/01/2011	16/05/2011		18 ± 6	628.5	326	3487	32 ± 12	29 ± 37	×	-409	7%	14.6 ± 9
2011_10	F	24/02/2011	16/05/2011		20 ± 9	330	250	3041	37 ± 11	35 ± 28	×	-37	0%	14.5 ± 8
2012_1	M	23/01/2012	14/09/2012		18 ± 6	523	291	9799	43 ± 18	31 ± 28	×	-434	19%	10.6 ± 11.1
2012_3	M	23/01/2012	26/04/2012		24 ± 6	454	277	4297	45 ± 11	36 ± 38	×	-286	1%	13.2 ± 6.2
2012_2	F	07/02/2012	28/09/2012	9	20 ± 9	303	233	7178	31 ± 12	28 ± 21	×	-58	1%	17 ± 9.1
2013_1	F	27/02/2013	19/10/2013	10	18 ± 6	340	262	8079	34 ± 9	43 ± 30	×	-130	2%	17.5 ± 10.4
2013_2	M	08/03/2013	02/11/2013	11	17 ± 10	1100	370	8321	39 ± 17	33 ± 41	×	-482	6%	17.4 ± 10.5
2013_3	M	10/02/2013	17/03/2013		22 ± 9	468	280	1513	46 ± 9	67 ± 41	×	-140	19%	7.2 ± 5.7
2013_4	M	03/03/2013	09/09/2013	9	18 ± 7	850	333	6064	35 ± 12	36 ± 36	×	-699	9%	18.1 ± 11.5
2013_5	F	24/02/2013	17/12/2013	9 (S)	22 ± 8	336	254	11732	43 ± 16	29 ± 27	×	-745	8%	16 ± 11.9
2013_7	F	17/02/2013	13/10/2013		19 ± 7	410	248	9204	42 ± 14	43 ± 36	×	-256	9%	15.1 ± 10.7
2013_9	M	11/02/2013	14/03/2013		24 ± 6	470	300	1517	47 ± 15	63 ± 45	×	-157	9%	9.1 ± 5.8
2013_11	M	11/02/2013	08/10/2013		23 ± 7	556	256	10151	44 ± 13	22 ± 32	×	-962	9%	12 ± 8.1
2013_12	M	17/02/2013	07/10/2013	10	19 ± 7	1150	375	7728	36 ± 12	31 ± 21	×	-164	5%	23.3 ± 10
2013_13	M	10/02/2013	20/04/2013		23 ± 6	600	321	3501	50 ± 17	50 ± 37	×	-221	18%	6.8 ± 6
2013_14	M	17/03/2013	24/11/2013	11	20 ± 8	300	270	10074	42 ± 16	19 ± 32	×	-743	19%	15 ± 11.2
2013_15	F	10/02/2013	29/09/2013	10	20 ± 7	366	248	8335	38 ± 9	47 ± 26	×	-121	2%	17.8 ± 10.3
2013_18	F	07/02/2013	03/08/2013		23 ± 9	346	255	6723	41 ± 15	34 ± 30	×	-192	1%	21.6 ± 8.5
2014_1	F	28/01/2014	21/09/2014	6 (E)	17 ± 6	265	250	7760	35 ± 9	38 ± 25		136		
2014_2	F	25/01/2014	30/03/2014		24 ± 10	304	255	2793	48 ± 15	56 ± 31	×	-34	20%	8.3 ± 6.3
2014_3	F	25/01/2014	04/10/2014	10	16 ± 6	293	244	7038	29 ± 8	28 ± 21	×	-64	0%	28 ± 10.1
2014_4	F	30/01/2014	12/03/2014		22 ± 9	265	236	1840	45 ± 13	57 ± 32		31		
2014_5	F	27/01/2014	23/09/2014		18 ± 4	244	240	7836	37 ± 8	23 ± 18		256		
2014_6	F	28/01/2014	30/09/2014	9	19 ± 6	266	243	8241	36 ± 10	32 ± 23	×	-128	1%	22.7 ± 9.2

ID	Sex	Dive start date	Dive end date	Date of re-turn	Nb. of location/day	Weight (kg)	Length (cm)	Total dives	Nb. dives/day	Dist./day (km)	Visit sea ice	Max dist. to sea ice (km)	Shallow dives in sea ice (%)	Hunting time/dive in sea ice (min)
2014_7	M	26/12/2013	23/10/2014	7 (S)	19 ± 9	405	277	11722	46 ± 21	32 ± 32	×	-857	20%	9.1 ± 8.3
2014_8	F	30/01/2014	21/09/2014		17 ± 6	270	247	7249	34 ± 10	28 ± 25	×	-203	3%	21.2 ± 10.1
2014_9	M	29/12/2013	11/09/2014		12 ± 6	700	322	4233	22 ± 10	35 ± 32	×	-195	3%	23.5 ± 11.1
2014_10	M	27/12/2013	27/09/2014	6 (N)	14 ± 8	700	306	7876	35 ± 14	27 ± 36	×	-241	12%	14.5 ± 8.7
2014_11	F	29/01/2014	17/09/2014		24 ± 13	295	249	8346	38 ± 19	28 ± 26	×	-148	9%	14.7 ± 9.2
Mean ± SD					**18 ± 9**				**39 ± 17**	**34 ± 31**			**12**	**14 ± 11**
Sum								**286843**						
Mean ± SD males						**559 ± 244**	**293 ± 39**		**41 ± 19**	**32 ± 35**		**-337 ± 267 (min males = -962)**	**10 ± 6**	**13 ± 10**
Mean ± SD fe-males						**307 ± 52**	**245 ± 13**		**37 ± 14**	**35 ± 28**		**-128 ± 195 (min fe-males = -745)**	**4 ± 5**	**17 ± 11**

Seasonal cycle of a 7 year time-series of sea ice concentration

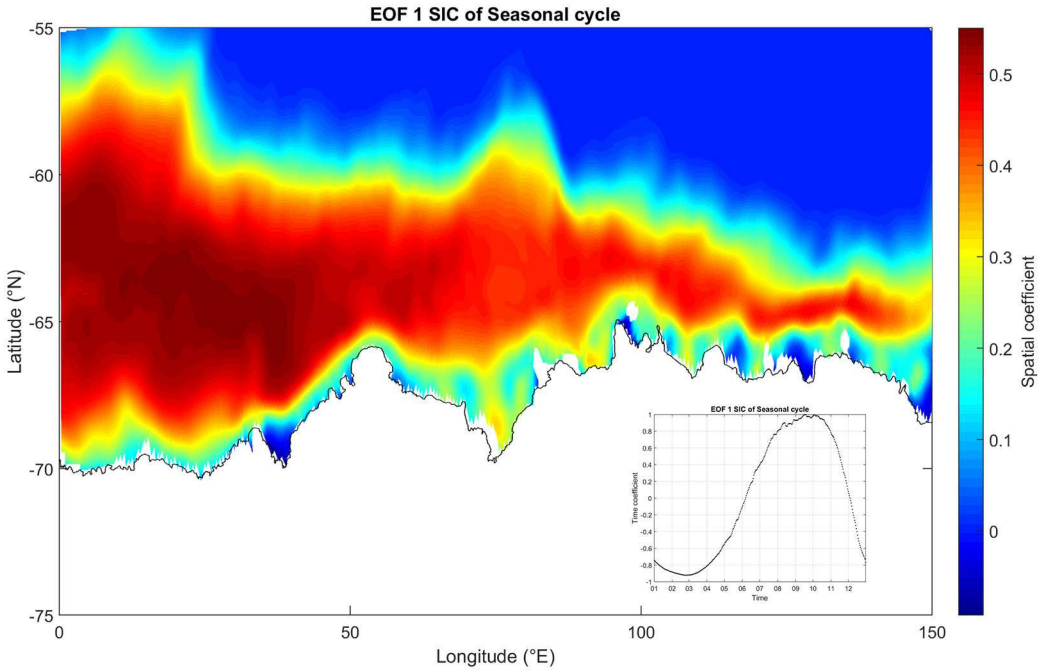


Figure BX1: Description of the seasonal signal of sea ice concentration within the study area represented by the spatial and temporal pattern from an Empirical Orthogonal Function analysis over a 7 year time-series of sea ice concentration.

Seasonal cycle in the spatial variability of high sea ice concentration around the seal position: computation of the anomaly

Computation of the anomaly of the spatial variability, $A'_{80\%}$: From March to August-September, an increase of $A_{80\%}$ with time was observed for males and females (Figure BX2A - B); we defined $A'_{80\%}$ by (i) computing the median of the observations from the time-series of $A_{80\%}$ for males and females (black lines, Figure BX2A – B), (ii) removing this median from each observation to obtain the anomaly of the spatial variability from its seasonal cycle (hereafter denoted $A'_{80\%}$).

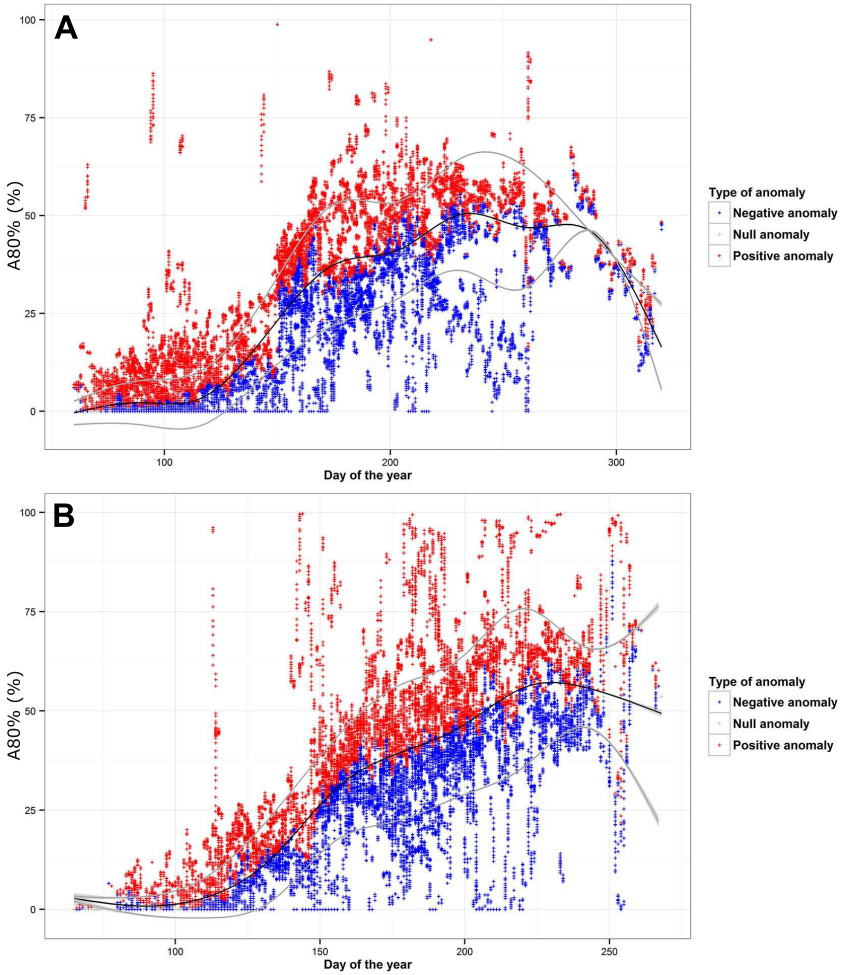


Figure BX2: Time series of $A_{80\%}$; the area covered by sea ice with concentration above 80% within a 50 km radius around the animal) for A) males and B) females. The time-series only includes positions inside the sea ice from March to the end of post-moult trips. The black line represents the median of the observations (used to compute the anomaly of the spatial variability from its seasonal cycle; $A'_{80\%}$), and grey lines represent the standard deviation associated with the median. Red dots correspond to positive local anomalies (observations superior to the median) while blue dots correspond to negative local anomalies (observations inferior to the median).

Model suites

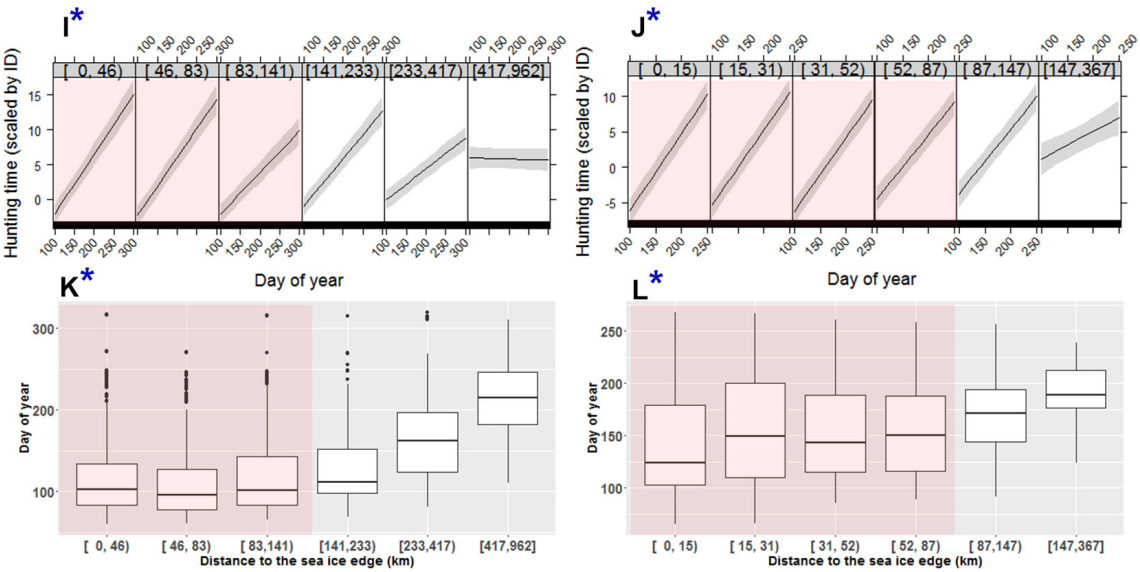


Figure BX3: Model 2, relationships from the two LMMs between hunting time and the same variables used in model 1 (Figure 8) except the spatial variability of concentrated sea ice patches ($A_{80\%}$) was replaced by the day of year. We choose to present only results for the modified variable as results are identical for other variables. Results for males are presented on the left panels and those for females on the right. Each graph from models shows the relationship relative to bin of the distance of the animal from the sea ice edge when inside sea ice (in km). For each graph, the thick lines represent the predictive values from the population at a given position in sea ice and the grey shaded envelopes represent the boundaries of the variation between the predicted values per individual. Available data for each bin of distance are represented by boxplots. The marginal ice zone is shown by the red shaded area.

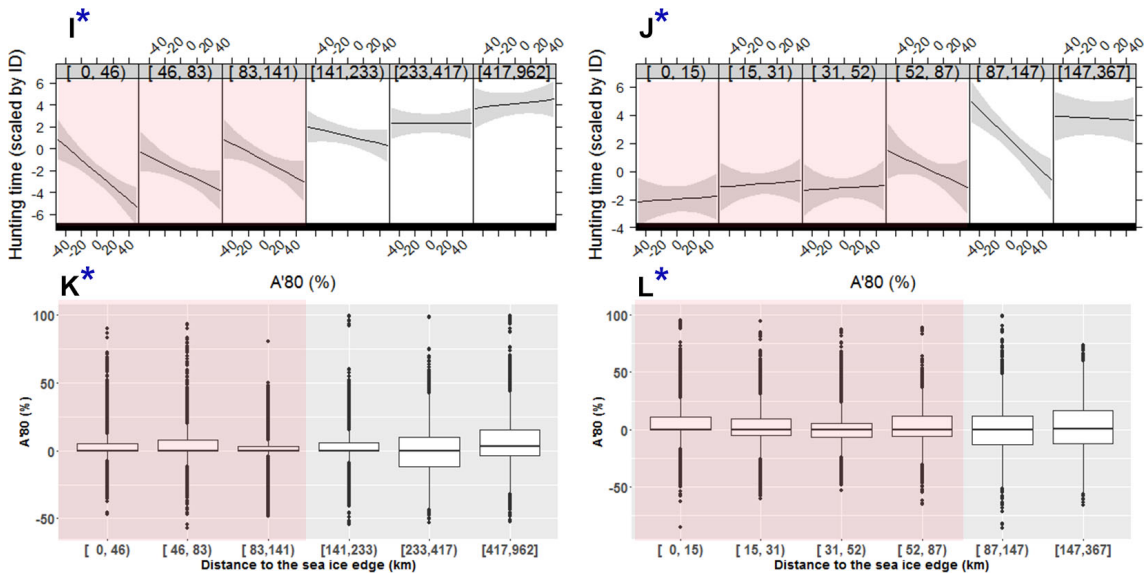


Figure BX4: Model 3, relationships from the two LMMs between hunting time and the same variables used in model 1 (Figure 8) except the spatial variability of concentrated sea ice patches ($A_{80\%}$) was replaced by the anomaly of the spatial variability of concentrated sea ice patches ($A'_{80\%}$). We choose to present only results for the modified variable as results are identical for other variables. Results for males are presented on the left panels and those for females on the right. Each graph from models shows the relationship relative to bin of the distance of the animal from the sea ice edge when inside sea ice (in km). For each graph, the thick lines represent the predictive values from the population at a given position in sea ice and the grey shaded envelopes represent the boundaries of the variation between the predicted values per individual. Available data for each bin of distance are represented by boxplots. The marginal ice zone is shown by the red shaded area.

Relationship between diving depth, bottom topography and distance from the sea ice edge

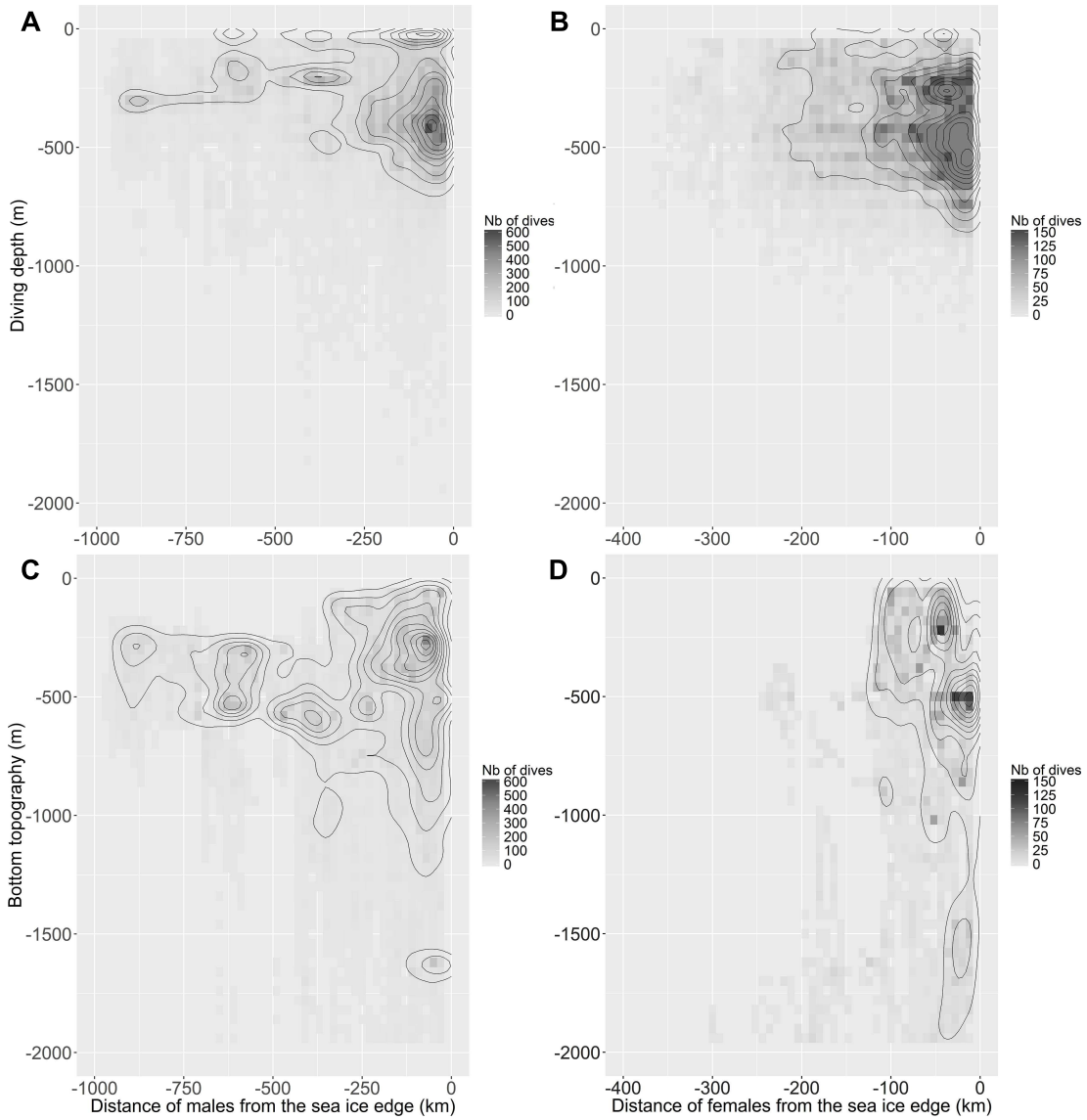


Figure BX5: Plot of diving depths (m) and bottom topography under the position of A and C) males and B and D) females relative to their distance from the sea ice edge (km) using a 2D kernel density estimation (*kde2D* function from package *MASS*, from R Development Core Team). One contour is drawn every 25 dives for females and 100 dives for males.

APPENDIX C

Table CX1: General information of the 43 post-moulting SESs (22 males and 21 females). It includes sex, dive start and end date, date of return when the tag did not stopped, number of Argos position transmitted daily, animal weight and snout-to-tail length upon deployment, total number of dives, mean number of dives per day and mean distance travelled per day between the first and last locations of each day. Additional information on behaviour towards sea ice is also included such as their maximal distance from the sea ice edge and their hunting time per dive. Negative distances refer to distances into the pack from the ice edge, and positive distances refer to distances north of the ice edge. Mean are expressed ± SD. Finally, individuals not included in all analysis are detailed in the analysis column.

ID	Sex	Start date	End date	Date of return	Nb. of location per day	Weight (kg)	Length (cm)	Total dives	Nb. dives per day	Dist. per day (km)	Max dist. to sea ice (km)	Hunting time per dive (min)	Analysis
2004_1	M	04/03/2004	29/03/2004		8 ± 4	368	250	553	25 ± 12	75 ± 49	-62	5.4 ± 3.9	×
2004_2	M	27/02/2004	09/07/2004		18 ± 7	385.5	267	6133	46 ± 20	34 ± 33	-192	11.3 ± 7.3	×
2004_3	F	01/03/2004	19/07/2004		14 ± 9	297.5	233	5363	38 ± 20	34 ± 29	-345	14.6 ± 11.3	×
2004_5	M	25/02/2004	06/08/2004		17 ± 6	469.5	282	7209	46 ± 18	22 ± 31	-341	14 ± 10	×
2004_6	F	22/02/2004	07/08/2004		12 ± 6	347	240	4248	27 ± 12	28 ± 26	-165	22 ± 10.2	×
2004_7	F	29/02/2004	02/08/2004		15 ± 9	295.5	238	6021	40 ± 19	42 ± 28	-110	8.5 ± 4	×
2004_8	M	27/02/2004	08/08/2004	6 then South	17 ± 9	274	235	7530	50 ± 25	40 ± 34	-610	5.4 ± 4.7	×
2004_10	F	29/02/2004	08/08/2004		16 ± 10	363.5	258	7503	46 ± 24	31 ± 29	-367	13 ± 10	×
2008_1	M	01/01/2008	08/09/2008		9 ± 5	266	230	8815	39 ± 30	33 ± 26	-161	10 ± 7.5	×
2008_2	F	24/12/2007	27/05/2008		14 ± 7	169	200	6031	39 ± 16	44 ± 30	-8	-	Only used in sea ice advance analysis
2008_6	F	24/01/2008	16/08/2008		11 ± 4	290	242	6200	31 ± 10	42 ± 26	-3	11.3 ± 6.2	×
2008_7	F	27/01/2008	11/07/2008		15 ± 7	377	267	5253	32 ± 13	44 ± 32	-244	17 ± 9.8	×
2009_16	M	01/01/2009	03/06/2009	6	17 ± 7	258	249	5887	40 ± 18	34 ± 28	-155	9.4 ± 7	×
2011_4	M	31/01/2011	16/05/2011		26 ± 7	800	330	4438	42 ± 11	33 ± 39	-316	13.5 ± 7.1	×
2011_6	F	19/02/2011	16/05/2011		31 ± 9	284.6	233	4230	50 ± 11	32 ± 31	-4	10.6 ± 5.8	Absent in sea ice advance analysis
2011_7	M	26/01/2011	15/04/2011		34 ± 10	452.5	280	4749	60 ± 19	36 ± 39	-302	9.3 ± 6.5	×
2011_9	M	27/01/2011	16/05/2011		18 ± 6	628.5	326	3487	32 ± 12	29 ± 37	-409	14.6 ± 9	×
2011_10	F	24/02/2011	16/05/2011		20 ± 9	330	250	3041	37 ± 11	35 ± 28	-37	14.5 ± 8	×
2012_1	M	23/01/2012	14/09/2012		18 ± 6	523	291	9799	43 ± 18	31 ± 28	-434	10.6 ± 11.1	×
2012_3	M	23/01/2012	26/04/2012		24 ± 6	454	277	4297	45 ± 11	36 ± 38	-286	13.2 ± 6.2	×
2012_2	F	07/02/2012	28/09/2012	9	20 ± 9	303	233	7178	31 ± 12	28 ± 21	-58	17 ± 9.1	×
2013_1	F	27/02/2013	19/10/2013	10	18 ± 6	340	262	8079	34 ± 9	43 ± 30	-130	17.5 ± 10.4	×
2013_2	M	08/03/2013	02/11/2013	11	17 ± 10	1100	370	8321	39 ± 17	33 ± 41	-482	17.4 ± 10.5	×
2013_3	M	10/02/2013	17/03/2013		22 ± 9	468	280	1513	46 ± 9	67 ± 41	-140	7.2 ± 5.7	×
2013_4	M	03/03/2013	09/09/2013	9	18 ± 7	850	333	6064	35 ± 12	36 ± 36	-699	18.1 ± 11.5	×
2013_5	F	24/02/2013	17/12/2013	9 then South	22 ± 8	336	254	11732	43 ± 16	29 ± 27	-745	16 ± 11.9	×
2013_7	F	17/02/2013	13/10/2013		19 ± 7	410	248	9204	42 ± 14	43 ± 36	-256	15.1 ± 10.7	×

ID	Sex	Start date	End date	Date of return	Nb. of location per day	Weight (kg)	Length (cm)	Total dives	Nb. dives per day	Dist. per day (km)	Max dist. to sea ice (km)	Hunting time per dive (min)	Analysis
2013_9	M	11/02/2013	14/03/2013		24 ± 6	470	300	1517	47 ± 15	63 ± 45	-157	9.1 ± 5.8	×
2013_11	M	11/02/2013	08/10/2013		23 ± 7	556	256	10151	44 ± 13	22 ± 32	-962	12 ± 8.1	×
2013_12	M	17/02/2013	07/10/2013	10	19 ± 7	1150	375	7728	36 ± 12	31 ± 21	-164	23.3 ± 10	×
2013_13	M	10/02/2013	20/04/2013		23 ± 6	600	321	3501	50 ± 17	50 ± 37	-221	6.8 ± 6	×
2013_14	M	17/03/2013	24/11/2013	11	20 ± 8	300	270	10074	42 ± 16	19 ± 32	-743	15 ± 11.2	×
2013_15	F	10/02/2013	29/09/2013	10	20 ± 7	366	248	8335	38 ± 9	47 ± 26	-121	17.8 ± 10.3	×
2013_18	F	07/02/2013	03/08/2013		23 ± 9	346	255	6723	41 ± 15	34 ± 30	-192	21.6 ± 8.5	×
2014_2	F	25/01/2014	30/03/2014		24 ± 10	304	255	2793	48 ± 15	56 ± 31	-34	8.3 ± 6.3	×
2014_3	F	25/01/2014	04/10/2014	10	16 ± 6	293	244	7038	29 ± 8	28 ± 21	-64	28 ± 10.1	×
2014_4	F	30/01/2014	12/03/2014		22 ± 9	265	236	1840	45 ± 13	57 ± 32	31	-	Only used in sea ice advance analysis
2014_6	F	28/01/2014	30/09/2014	9	19 ± 6	266	243	8241	36 ± 10	32 ± 23	-128	22.7 ± 9.2	×
2014_7	M	26/12/2013	23/10/2014	7 then South	19 ± 9	405	277	11722	46 ± 21	32 ± 32	-857	9.1 ± 8.3	×
2014_8	F	30/01/2014	21/09/2014		17 ± 6	270	247	7249	34 ± 10	28 ± 25	-203	21.2 ± 10.1	×
2014_9	M	29/12/2013	11/09/2014		12 ± 6	700	322	4233	22 ± 10	35 ± 32	-195	23.5 ± 11.1	×
2014_10	M	27/12/2013	27/09/2014	6 then North	14 ± 8	700	306	7876	35 ± 14	27 ± 36	-241	14.5 ± 8.7	×
2014_11	F	29/01/2014	17/09/2014		24 ± 13	295	249	8346	38 ± 19	28 ± 26	-148	14.7 ± 9.2	×
Mean ± SD or sum	_	_	_		**18 ± 9**	_	_	**273542**	**39 ± 17**	**34 ± 31**		**14 ± 10**	_
Mean ± SD or sum males	_	_	_		_	**554 ± 248**	**292 ± 40**	**135534**	**41 ± 19**	**32 ± 34**	**-370 ± 254 (min males = -962)**	**13 ± 10**	_
Mean ± SD or sum females	_	_	_		_	**312 ± 51**	**245 ± 14**	**138008**	**38 ± 15**	**36 ± 28**	**-159 ± 174 (min females = -745)**	**17 ± 11**	_

APPENDIX D

Table DX1: General information of the 23 post-moulting Kerguelen male SESs. It includes dive start and end date, date of return when the tag did not stopped, animal weight (expressed in kg) and snout-to-tail length upon deployment (expressed in cm), if the CTD (Conductivity-Temperature-Depth) data were usable for analysis, number of Argos position transmitted daily, total number of dives, mean number of dives per day and mean distance travelled per day between the first and last locations of each day (expressed in km), if the animal visited polynyas during its trip, total number of CTD profiles, and number of CTD profile per day. Mean are expressed ± SD.

ID	Dive start	Dive end	Month return	Weight	Length	CTD	Nb. of positions/day	Total dives	Dives/day	Dist./day	Inside polynyas	CTD profiles/day	Total CTD profiles
2004_1	04/03/2004	29/03/2004		368	250	No	8 ± 4	553	25 ± 12	75 ± 49	No		
2004_2	27/02/2004	09/07/2004		385,5	267	x	18 ± 7	6133	46 ± 20	34 ± 33	x	2.9 ± 1	336
2004_5	25/02/2004	06/08/2004		469.5	282	x	17 ± 6	7209	46 ± 18	22 ± 31	x	2.7 ± 1	371
2004_8	27/02/2004	08/08/2004	6 then South	274	235	x	17 ± 9	7530	50 ± 25	40 ± 34	x	2.5 ± 1	343
2008_1	01/01/2008	08/09/2008		266	230	No	9 ± 5	8815	39 ± 30	33 ± 26	x		
2009_16	01/01/2009	03/06/2009	6	258	249	x	17 ± 7	5887	40 ± 18	34 ± 28	No	1.9 ± 0.3	266
2011_1	27/01/2011	20/02/2011		680	316	x	21 ± 7	1002	40 ± 13	98 ± 30	No	1.8 ± 0.4	42
2011_4	31/01/2011	16/05/2011		800	330	x	26 ± 7	4438	42 ± 11	33 ± 39	x	1.9 ± 0.4	411
2011_7	26/01/2011	15/04/2011		452.5	280	x	34 ± 10	4749	60 ± 19	36 ± 39	x	1.7 ± 0.5	104
2011_9	27/01/2011	16/05/2011		628.5	326	x	18 ± 6	3487	32 ± 12	29 ± 37	x	1.8 ± 0.4	407
2012_1	23/01/2012	14/09/2012		523	291	x	18 ± 6	9799	43 ± 18	31 ± 28	x	3.2 ± 0.8	737
2012_2	23/01/2012	26/04/2012		454	277	x	24 ± 6	4297	45 ± 11	36 ± 38	x	3.4 ± 0.8	321
2013_2	08/03/2013	02/11/2013	11	1100	370	x	17 ± 10	8321	39 ± 17	33 ± 41	x	3.3 ± 0.8	627
2013_3	10/02/2013	17/03/2013		468	280	x	22 ± 9	1513	46 ± 9	67 ± 41	x	3.2 ± 0.8	105
2013_4	03/03/2013	09/09/2013	9	850	333	x	18 ± 7	6064	35 ± 12	36 ± 36	No	3 ± 1	560
2013_9	11/02/2013	14/03/2013		470	300	x	24 ± 6	1517	47 ± 15	63 ± 45	x	3.5 ± 0.6	111
2013_11	11/02/2013	08/10/2013		556	256	x	23 ± 7	10151	44 ± 13	22 ± 32	x	3.2 ± 0.8	730
2013_12	17/02/2013	07/10/2013	10	1150	375	x	19 ± 7	7728	36 ± 12	31 ± 21	No	3.0 ± 0.9	657
2013_13	10/02/2013	20/04/2013		600	321	x	23 ± 6	3501	50 ± 17	50 ± 37	x	3.4 ± 0.8	220
2013_14	17/03/2013	24/11/2013	11	300	270	x	20 ± 8	10074	42 ± 16	19 ± 32	x	3.2 ± 0.8	660
2014_7	26/12/2013	23/10/2014	7 then South	405	277	x	19 ± 9	11722	46 ± 21	32 ± 32	x	3.4 ± 0.7	413
2014_9	29/12/2013	11/09/2014		700	322	x	12 ± 6	4233	22 ± 10	35 ± 32	x	2.6 ± 1	471
2014_10	27/12/2013	27/09/2014	6 then North	700	306	x	14 ± 8	7876	35 ± 14	27 ± 36	x	3. ± 0.9	676
Mean ± SD				**559 ± 244**	**293 ± 39**		**18 ± 9**		**41 ± 19**	**32 ± 34**		**2.8 ± 1**	
Sum						**21**		**136599**			**18**		**8568**

Change in dive durations inside and outside polynyas and within the different cores of the polynya on the Antarctic shelf region.

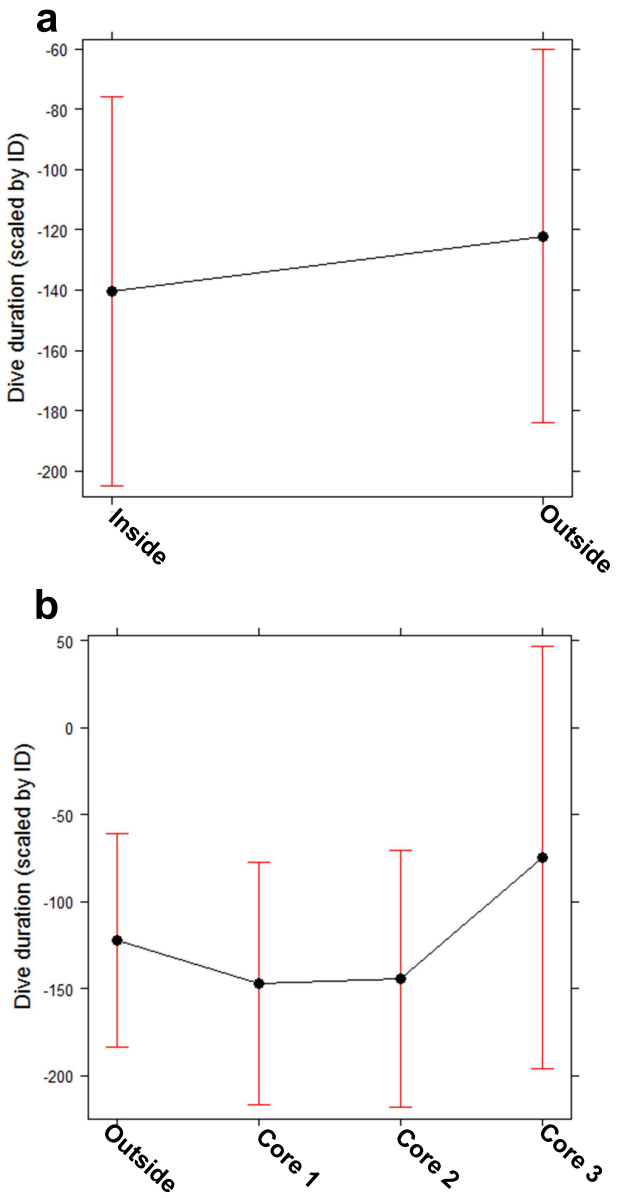


Figure DX1: Change in dive durations inside and outside polynyas and within the different cores of the polynya on the Antarctic shelf region. Relationships from the two LMMs between maximal dive duration and the position of the seal inside versus outside and the position of the seal outside and in the core 1, 2 and 3 are represented in the panel (**a**) and (**b**) respectively. LMMS were computed based on CTD data at the bottom phase of dives (17 SESs inside polynyas on the shelf and 20 SESs outside polynyas on the shelf as CTD data were not available for the individual 2004-1 and 2008-1).

Influence of the polynya size and its variability on seals' polynya use and foraging activity

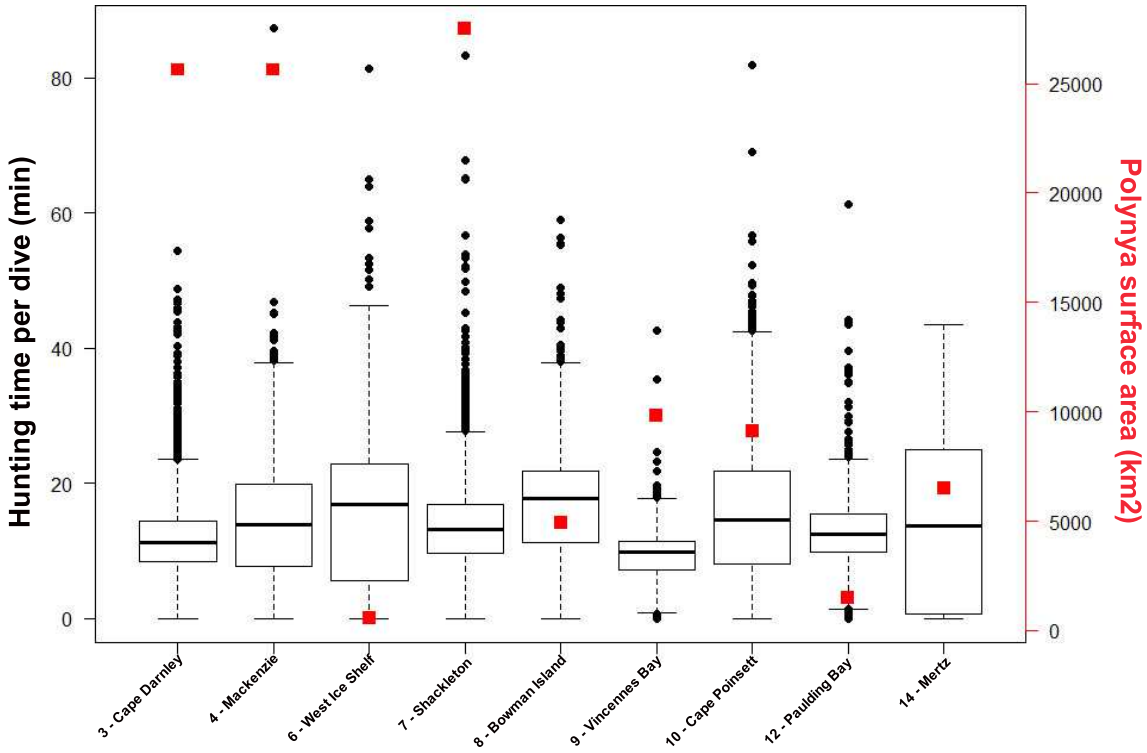


Figure DX2: Relation between polynya maximal surface extent area and SES hunting time per dive. Boxplots of hunting time per dive (expressed in minutes) are represented for each of the 9 polynyas visited by the 18 SESs from 2004 to 2014. The red squares indicate the maximal surface extent area (expressed in km^2) for each polynya based on the larger yearly sea ice production contour (2.5 $m.y^{-1}$).

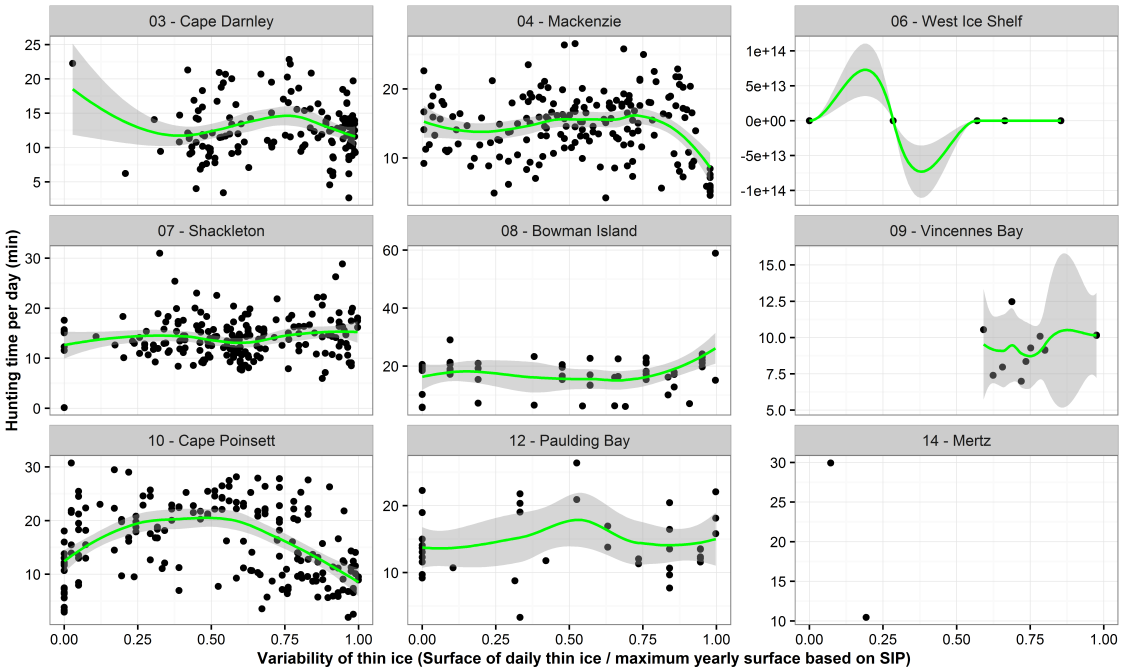


Figure DX3: Relation between the variability of polynya surface extent area at a daily scale and SES hunting time per dive averaged per day. Scatter plots representing hunting time per dive (expressed in minutes) averaged per day for each of the 9 polynyas visited by the 18 SESs from 2004 to 2014 in relation with the variability in surface extent area of polynya. The variability is expressed as thin ice variability, in a given polynya it represents the division of the daily thin ice surface extent area (defined by thin ice thickness above 0 and inferior to 0.2 m) by the maximal surface extent area for the given polynya (based on the larger yearly sea ice production contour (2.5 $m.y^{-1}$). The green line represents a smoothed conditional mean of the observations by fitting a polynomial regression using least squares with the package *ggplot2* and the argument *geom smooth* from R Development Core Team. The grey bandwidth represents the 95% confidence level interval for predictions. Lack of observations for polynyas 6, 9 and 14 led to the absence or incorrect smoothed means.

APPENDIX E

Bio-physical characterisation of East Antarctic polynyas as key southern elephant seal (*Mirounga leonina*) foraging habitat

Veda Malpress[1,2*], Sophie Bestley[1,2,3], Stuart Corney[2], Dirk Welsford[3], Sara Labrousse[1,4], Michael Sumner[2,3] and Mark Hindell[1,2]

[1]*Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania 7001 Australia*
[2]*Antarctic Climate & Ecosystem Cooperative Research Centre, University of Tasmania, Hobart, Tasmania 7001 Australia*
[3]*Australian Antarctic Division, Department of Environment, Kingston, Tasmania 7050 Australia*
[4]*Sorbonne Universités, UPMC Univ., Paris 06, UMR 7159 CNRS-IRD-MNHN, LOCEAN-IPSL, 75005 Paris, France*
**Email: vedam@utas.edu.au*

Abstract

Antarctic coastal polynyas are persistent open water areas in the sea ice zone, and regions of high biological productivity thought to be important foraging habitat for marine predators. This study quantified southern elephant seal (*Mirounga leonina)* habitat usage within and around the polynyas of the Prydz Bay region in East Antarctica, and examined the bio-physical characteristics structuring polynyas as foraging habitat. A climatological regional ocean model (ROMS) was used to provide context for *in situ* temperature-salinity vertical profiles collected by tagged elephant seals and to characterise the physical properties structuring polynyas. Biological properties were explored using remotely-sensed surface chlorophyll and, qualitatively, historical fish assemblage data. Spatially gridded residence time of seals was examined in relation to habitat characteristics using generalized additive mixed models. The results showed clear polynya usage during early autumn (post-moult 1) and increasingly concentrated usage during early winter (post-moult 2). Bathymetry, Chl-*a*, surface net heat flux (or polynya location) and bottom temperature were identified as significant bio-physical predictors of the spatio-temporal habitat usage. The findings from this study confirm polynyas as important marine habitats for southern elephant seals. A hypothesis is advanced that the bio-physical coupling from surface to subsurface productivity, supporting elevated rates of secondary production, is likely to extend throughout the water column as it becomes fully convected during autumn-winter, to also promote pelagic-benthic linkages important for benthic foraging within polynyas.

Key words: polynyas; East Antarctica; Prydz Bay; *Mirounga leonina*; habitat usage; ROMS.

Introduction

Antarctic coastal polynyas are areas of reduced sea ice cover within the coastal sea ice zone, largely maintained by offshore winds and oceanic currents advecting ice away from the coast [1]. Although constituting a relatively small area of the Southern Ocean (~ 1% of maximum sea ice area), coastal polynyas are responsible for an estimated 10% of sea ice production. The brine rejection as a result of ice formation can lead to Dense Shelf Water (DSW) formation on the continental shelf [2-4]. In key areas this may flow off-shelf to form Antarctic Bottom Water (AABW). AABW formation is one important process driving the global thermohaline (overturning) circulation and acts as a sink for both heat and CO_2 [5, 6].

Due to the ice-free environment, particularly in early spring when solar radiation rapidly increases, polynyas are regions of enhanced oceanic primary and secondary production relative to surrounding habitat [7]. Consequently, polynyas also support relatively high densities of upper trophic level organisms [8]. Foraging of several important Antarctic predators, such as Antarctic fur seals, Weddell seals, Adelie penguins and southern elephant seals, is documented in polynya regions [9, 10]. To better understand why polynyas are important to top predators requires some understanding of the processes operating within polynyas that lead to the concentration and/or increase in food availability.

A major constraint to polynya research has been the difficulty in observing water properties under the ice covered regions. This is due to a combination of a lack of access by ships for much of the year [5], expense and logistical difficulty in deployment and recovery of mooring arrays [11] and the limited ability of satellites to remotely sense the water surface properties when it is covered by dynamic ice [12]. Investigating circulation processes is possible through the development of high-resolution ocean models such as the Regional Ocean Modelling System (ROMS) [13]. However, *in situ* observations are essential for verifying and constraining circulation models.

Marine predators equipped with oceanographic sensors provide a solution to the lack of *in situ* observations, providing information on ocean structure and water mass processes in regions and seasons rarely observed with traditional oceanographic platforms [12, 14]. Southern elephant seals (*Mirounga leonina*, or SES) are far-ranging, deep-diving predators that regularly spend time within the sea ice environment and high-latitude waters during their lengthy post-moult foraging trips [15-17]. Conductivity-Temperature-Depth Satellite Relay Data Loggers (CTD SRDLs) are used to simultaneously record animal location, dive behaviour and hydrographic profiles [12]. The data can provide insight into animal behaviour [e.g. 16, 17] as well as *in situ* environmental information [e.g. 5, 9, 12, 18] over extended timescales.

Such tagging studies have significantly increased understanding of the use of oceanographic features by foraging seals, showing SES widely exploit oceanic frontal systems, the marginal and pack-ice and coastal shelf regions, and can display both pelagic and benthic diving behaviour [16, 17, 19-21]. During the post-moult migrations some individuals of the Kerguelen and Macquarie Island populations forage along the East Antarctic shelf region [5, 12, 16, 22], and various foraging indices (*e.g.* body condition, patch quality, prey encounter events) indicate this may comprise the most lucrative foraging habitat [16, 22, 23].

While studies of SES foraging behaviour have identified the importance of on-shelf regions in East Antarctica, the importance of specific habitat features within the region, such as polynyas, and the properties structuring these, have not been fully explored. This study aims to provide a bio-physical characterisation of polynyas as foraging habitat for SES specifically within the greater Prydz Bay region (63°E– 88°E) (Fig 1). Here, four coastal polynyas (Cape Darnley, Mackenzie, Prydz Bay and West Ice Shelf) play an important role in the sea-ice cycle [18], with the Cape Darnley polynya responsible for the second highest rate of polynya sea-ice production around Antarctica [1]. Additionally, this region is characterised by high rates of primary productivity [7] and significant benthic diversity [24].

The *in situ* CTD data collected from tagged seals provides invaluable observations of ocean properties; however, these can only describe the water characteristics in locations where SES were present. A realisation of the Regional Ocean Modelling System (ROMS) was used to provide a more complete spatial context for the region [25]. Spatial bio-physical predictor fields, from ROMS and additionally satellite chlorophyll data are examined as explanatory variables for statistical models predicting seal residence time. The results are used to develop a general hypothesis regarding the underlying physical-biological and pelagic-benthic coupling that supports where and how foraging habitat for marine predators occurs.

Methodology

1. Data sources

The spatial extent of the greater Prydz Bay study region from 63°E to 88°E includes four significant polynyas: Cape Darnley, Mackenzie Bay, Prydz Bay and West Ice Shelf (nomenclature as per Arrigo and Dijken [7]), and the northern boundary of the study region was set at 65°S, in order to include the shelf break.

Several different datasets were integrated in this study. A ROMS implementation provided the regional oceanographic context for the *in situ* observations collected by instrumented seals, and the two were used in conjunction to investigate dynamics within the four polynyas of interest. Additional biological information was obtained from remotely-sensed surface chlorophyll data and an historical fish trawl database [26]. The habitat usage of seals within the greater Prydz Bay region was summarised as gridded residence time, as

calculated from complete telemetry tracks, and modelled in response to selected bio-physical predictor fields. These datasets and the approaches used are detailed in turn below.

1.1 Configuration of the Regional Ocean Modelling System (ROMS)

A climatological run of ROMS using present conditions (1992 – 2008) was used to provide oceanographic context for seal habitat. The implementation was circumpolar with a horizontal grid resolution of 0.25° and a northern boundary at 30° S; however, this study focused on the region described above. ROMS is a terrain following model, with 31 vertical levels that are concentrated towards the top and the bottom of the vertical domain. Daily atmospheric forcing was from the NCEPII reanalysis [27], with the northern boundary condition sourced from the ECCO2 reanalysis [28, 29]. The model used a mean state for surface initial condition and analytical initial conditions at depth.

This ROMS implementation used prescribed climatological surface heat and salt fluxes at the surface boundary, to simulate ice production and coverage. The flux climatology was derived using a model strongly forced using Special Sensor Microwave Imager (SSM/I) observations [1, 13]. This method forced heat and salt into the top of the water column [1] to overcome the poor performance of most ocean models in representing polynya locations and circulation processes. Model output was on a daily time step and depth-structured physical variables such as temperature, salinity, horizontal and vertical velocities were utilised.

1.2 Seal Conductivity-Temperature-Depth (CTD) casts

Conductivity-Temperature-Depth Satellite Relay Data loggers (CTD-SRDLs) (Sea Mammal Research Unit, University of St Andrews, UK) autonomously collect and summarise data and transmit via the ARGOS satellite system when animals surface. These data have been described in detail elsewhere [14, 30, 31], but briefly every vertical profile consists of temperature and salinity measurements at 17 depths (inflexion points) determined on-board by a “broken stick algorithm” [31]. The CTD data is post-processed [14] and publicly available through the Marine Mammals Exploring the Oceans Pole to Pole (MEOP) portal (www.meop.net/database). Animal handlings were performed in accordance with relevant guidelines and regulations, after approval by the University of Tasmania and Macquarie University's Animal Ethics Committees for Australian deployments and by the Institut Paul-Emile Victor (IPEV) Ethics Committee for French deployments. For further tagging and handling information, refer to Roquet *et al.* [14].

The Prydz Bay regional subset included 58 SES that visited the study region during 2007, 2009 and 2011-2015. This included both French and Australian deployments at Kerguelen Island (n = 16) and at Davis Station (n = 42), Antarctica. These comprised almost all juvenile/sub-adult males (and one female seal), so age effects were not considered. For the purposes of this study, population level habitat selection was the focus. The dataset was collated across all years to enable comparison with the climatological ROMS output and focus upon seasonal trends. For this, four periods were defined based on the distinct stages in the annual cycle of elephant seals [22, 32]; post-breeding (PB, November – January), post-moult 1 (PM1, February – April), post-moult 2 (PM2, May – July) and post-moult 3 (PM3, August – October). Due to the data availability (Table 1) for the purposes of statistical analysis only PM1 and PM2 are included.

1.3 Remotely sensed surface chlorophyll

To provide information about the biological characteristics of the study region, and in particular polynyas, surface chlorophyll (Chl-*a*) data was examined. Two climatological fields were constructed for the study domain from monthly 8km gridded SeaWiFS/MODIS remotely sensed images over the period November 1997 to October 2008 (http://oceandata.sci.gsfc.nasa.gov/SeaWiFS/Mapped/Monthly/9km/Chlor_a/) using the R (R core development team 2015) package *raadtools* [33]. The climatologies were defined based on the elephant seal seasons as described above. An average for the season *prior* to each of PM1 and PM2 was used in order to allow time for energy transfer between trophic levels.

1.4 Historical fish data

The available historical pelagic and benthic fish data [34] was collated from the demersal trawls (Otter and Beam) on two historical voyages, AAMBER1 (17/2 -5/3 1987) and AAMBER2 (17/2 – 28/2 1991) [26]. This dataset was spatially patchy but used as a qualitative indicator of species richness (total number of species) and approximate fish biomass within the region. There was greater availability of fish length records than weights within the database, and given that these parameters are related, length was used as a mass proxy. Total lengths for pelagic and benthic species were summed and divided by trawl effort; trawl effort was calculated from Speed (kn) x Tow Duration (min)/60.

2. ROMS characterisation of polynyas

An animation of ROMS daily surface temperatures, which shows activity especially within the Cape Darnley and Mackenzie polynyas, can be found in S1 Video.

2.1 Virtual moorings

Virtual moorings were used to ensure ROMS was adequately simulating oceanographic conditions, as well as to characterise each polynya's seasonal trends. Contours of net surface heat flux during the freezing season, March – October [1] were used to define the broader polynya region (Fig 1a) and a small centroid area defined for finer scale investigation. Due to the differing polynyas sizes the Cape Darnley and Mackenzie polynya centroids were a 3 x 3 (~0.75° x 0.75°) grid cell area, whereas Prydz polynya was 2 x 2 (~0.5° x 0.5°) and the West Ice shelf 1 x 2 (~0.25° x 0.5°). It was ensured that the grid cells were neither bordering land nor ice shelves as a precaution to avoid artefacts on the environmental variables of focus. Oceanographic time-series were constructed from ocean properties averaged across cells within the centroid regions, within the top and bottom 50 m of the water column. Supplementary time-series showing full-year temperatures and salinities at depth can be found in S1 Appendix.

2.2 Temperature-Salinity plots

Temperature-Salinity (T-S) plots were created to compare ROMS output with seal CTD data. All unique seal CTD casts were extracted from a heat flux contour larger than the centroid region (due to the differing activity intensities these thresholds differed: Cape Darnley = -150 W m^{-2}, Mackenzie = -210 W m^{-2}, Prydz Bay = -110 W m^{-2}, West Ice Shelf = -60 W m^{-2}) and combined for all years to display seasonal changes in the water column. Over the equivalent time period, a ROMS T-S profile was extracted for each grid cell within the centroid (e.g. 9 for Cape Darnley). The larger area of the contour was used to capture the SES data (see S2 Appendix), rather than the smaller ROMS centroid area, to account for potential error in position and to give a broader representation of polynya processes. A potential density surface (σ_2=37.16) was used to approximate the neutral density of AABW (γ_n=28.27) [2] and plotted together with the approximate freezing point of sea-water (-1.85°C).

2.3 Virtual transects

Spatial transects were constructed to further explore oceanographic conditions and seal distribution in and around polynyas. A transect running north-south from each polynya centroid was defined, ensuring the origin was at least two grid cells north of any land or ice shelves, and extending north past the shelf break. Each transect was 3 grid cells wide, approximating a width of 0.5° +/- 0.2°.

Temperature and salinity were averaged throughout the freezing period (March – October) and across longitude, but resolved vertically through the water column. The total number of individual seals and unique CTD casts were calculated per 0.25° grid cell along each transect to provide a visual representation of seal density and the quantity of available data in relation to the transect features. Full-year time-series animations of temperature along each polynya transect can be found in S2 – S5 Video.

3. Characterisation of SES habitat use

3.1 Spatial residence time

The ARGOS tracks for all SES (n = 58) were filtered using a Kalman filter [35] to minimise positional errors and to estimate location points along movement paths at regular 2-hour intervals [22]. From this the average residence time (hours) was calculated across all individual seals, on a regular 0.25° x 0.25° longitude/latitude grid within the study region, using the R package *trip* [36]. Results were calculated for both an annual average representation of time spent, and the two focal post-moult seasons (PM1 and PM2), and reprojected on to the ROMS grid for analyses. The size of Prydz Bay is small relative to the scale of seal migrations and as such the entire region was assumed to be equally available to SES [37]. This allowed for the simplifying assumption of modelling habitat usage without considering differing availability [37].

3.2 Statistical models

Habitat use (residence time) was modelled in response to a selected set of biophysical variables. Statistical models focused on PM1 and PM2 (separately) due to the majority of the data being present in these seasons (Table 1). Using the R package *mgcv* [38] initial models were tested fitting generalised additive models (GAMs) to the data, before fitting two final models as generalised additive mixed models (GAMMs) that incorporated a spatial correlation structure.

3.3 Predictor variables

A total of 9 predictor variables were initially considered for each season, comprising 8 physical variables extracted from ROMS plus the remotely sensed surface chlorophyll (Chl-*a*). These were: bathymetry, surface heat flux, surface temperature, bottom temperature, bottom velocity magnitude, the eastward (U), northward (V) and vertical (W) components of bottom velocity. Each of these was chosen because of their assumed relevance to structuring polynyas as foraging habitat.

The heat flux variable was averaged over the entire freezing period (March - October) to represent polynya location and intensity even post-activity *i.e.* during summer. This averaged heat flux was used to develop both PM1 and PM2 models. The magnitude of bottom velocity was calculated from $\sqrt{(u^2 + v^2)}$. As described above the chlorophyll predictor represented an average of the previous season. This decision was made to allow for a biological lag between primary production and the development of an ecological community. To account for skewed distributions, Chl-*a* and bathymetry were log-transformed; the response variable (residence time) was also log-transformed.

Correlation between predictor variables (collinearity) can present an issue when developing statistical models, with highly correlated predictors competing [39]. To limit any such effect, correlation between the variables was checked to ensure these were no greater than 0.8 (Fig S3.2 and S3.4, S3 Appendix). Variance inflation factors (VIFs), which indicate the increase in the estimated variance of model coefficients that may occur through collinearity [39] were also calculated and a maximum VIF of 3 allowed (Table S3.1 and S3.3). Once the appropriate set of predictor variables had been identified (*i.e.* selected predictor variables had both correlation and VIFs lower than the defined thresholds) Akaike's Information Criterion (AIC) [40] was used to build up models manually via a forward step procedure (only complete observations were used; PM1 n = 3408; PM2 n = 2448). This process was chosen to facilitate understanding of the contribution of individual terms. Initially, a generalised additive model (GAM) was fitted to each individual predictor and the variable with the smallest AIC value (indicating comparative model fit) selected as the first covariate. Further predictors were added until F-tests indicated non-significance (*i.e.* $p > 0.05$).

The final combination of predictors from each seasonal GAM was then used to build a GAMM for each of the seasons PM1 and PM2. These GAMMs included a Gaussian correlation structure on latitude and longitude to address the spatial autocorrelation inherent within the data [41]. The complete statistical procedure and results, including the partial

residual plots for the two final GAMMs, can be found in S3 Appendix. The fitted values from the final model for each season were mapped to show the predicted habitat usage across the greater Prydz Bay region.

Results

The CTD casts and tracking locations from the 58 seals (Table 1) provided information across most years between 2007 and 2015 (Table 2) with the majority of data (~90%) recorded during PM1 and PM2. This reflects that seals tend to arrive in the region early in the year and stay in the shelf region for varying lengths of time (see also S2 Appendix). Overall the CTD dataset provided good spatial coverage of the study region, with observations across the shelf, within all four polynyas, and along the shelf break (Fig 1b).

297 **Table 1: SES data summaries per season.**

	Season				
	PM1	**PM2**	**PM3**	**PB**	**Entire Dataset**
Years Available	2007, 2009, 2011 – 2015	2009, 2011 – 2013	2009, 2011 – 2013	2007, 2011 – 2015	2007, 2009, 2011 – 2015
Number of seals	57	29	11	9	58
Number of CTD Casts	9514	4185	1456	527	15682
Number of KF Locations	29936	10349	2302	410	42997

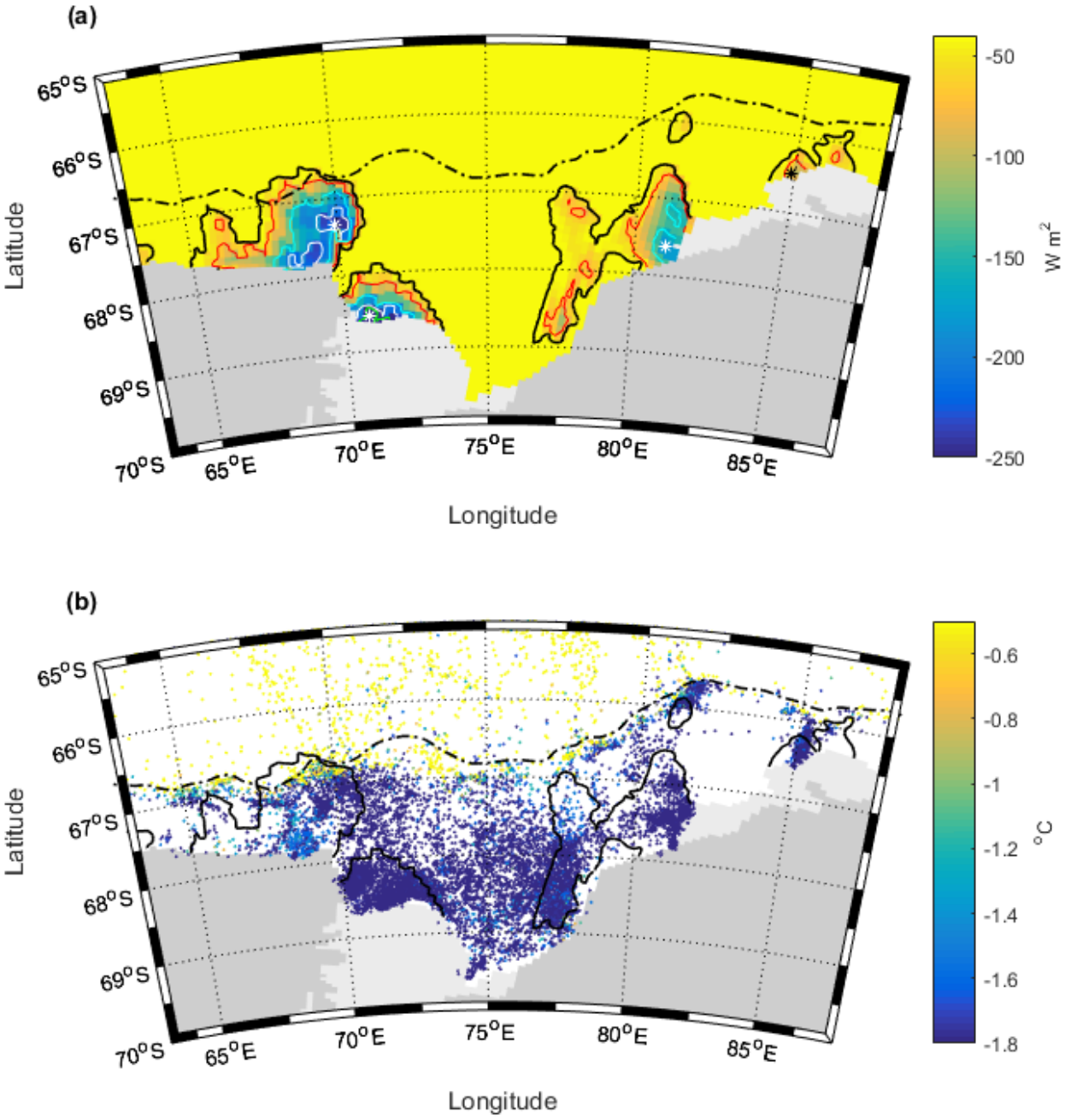
298 The years in which data was available and the number of seals are displayed, as well as the number of CTD casts and
299 Kalman filtered (KF) track locations (see Methods). PM1 = Post-moult 1 (Feb – Apr), PM2 = Post-moult 2 (May – Jul),
300 PM3 = Post-moult 3 (Aug – Oct) and PB = Post-breeding (Nov – Jan).

301

302 **Table 2: SES data summaries per polynya.**

Polynya	**Seals**	**Unique Casts**	**Total Weeks (Non Continuous)**	**Total Year**
Cape Darnley	20	817	36 (Jan – Nov)	2007, 2011 – 2015
Mackenzie	32	1649	18 (Feb – Sept)	2011 – 2013, 2015
Prydz	13	1642	33 (Mar – Nov)	2009, 2011 – 2012
West Ice Shelf	3	272	23 (May – Oct)	2013

303



304

305 **Fig 1. Map of the Prydz Bay study region.**

306 a) ROMS mean surface heat flux (expressed as W m^{-2}) during the freezing season (March to October) and b)
307 instrumented southern elephant seal CTD cast locations from the MEOP portal, 2007-2015 where data points
308 are coloured by the deepest temperature readings per cast. In panel a) Heat flux contours of -40 W m^{-2} (black), -
309 70 W m^{-2} (red), -150 W m^{-2} (cyan), -210 W m^{-2} (white) and -260 W m^{-2} (green) are shown. Polynyas from west
310 to east are Cape Darnley (70°E), Mackenzie (72°E), Prydz Bay (82°E) and West Ice shelf (85°E). Centroid
311 locations are indicated by a white or black star (Fig 1a).

312

1. ROMS evaluation

During the freezing period (March – October, Fig 1a) the polynyas were clearly far more active, in terms of a much greater negative heat flux, than the surrounding ocean. Mackenzie and Cape Darnley had the two most active cores, with a peak heat flux of -260 W m^{-2} and -210 W m^{-2} respectively. For the weaker Prydz and West Ice Shelf polynyas, the maximum average heat flux was -150 W m^{-2} and -70 W m^{-2} respectively. The polynyas centroids were defined within these contours.

1.1 Seasonal temperature and salinity trends

ROMS output for the four polynyas demonstrated a clear seasonal cycle of cooling and increasing salinity from the start of the freezing period (March-April), and the reverse in spring (mid-October; best seen in Fig 2d). A greater variability was evident in the top layer (Fig 2b and d) than the bottom layer (Fig 2a and c). The relationship between salinity and temperature was clear in both layers, with a temperature decrease corresponding to a salinity increase though with a slight lag. This lag was most noticeable in Cape Darnley and Mackenzie leading into the freezing season, where surface and bottom temperatures were at a minimum. As expected, Cape Darnley polynya was the coldest and most saline polynya and also showed the most variability within each month. This suggested that overall Cape Darnley was more dynamic, especially in the mid – late freezing season (May – October).

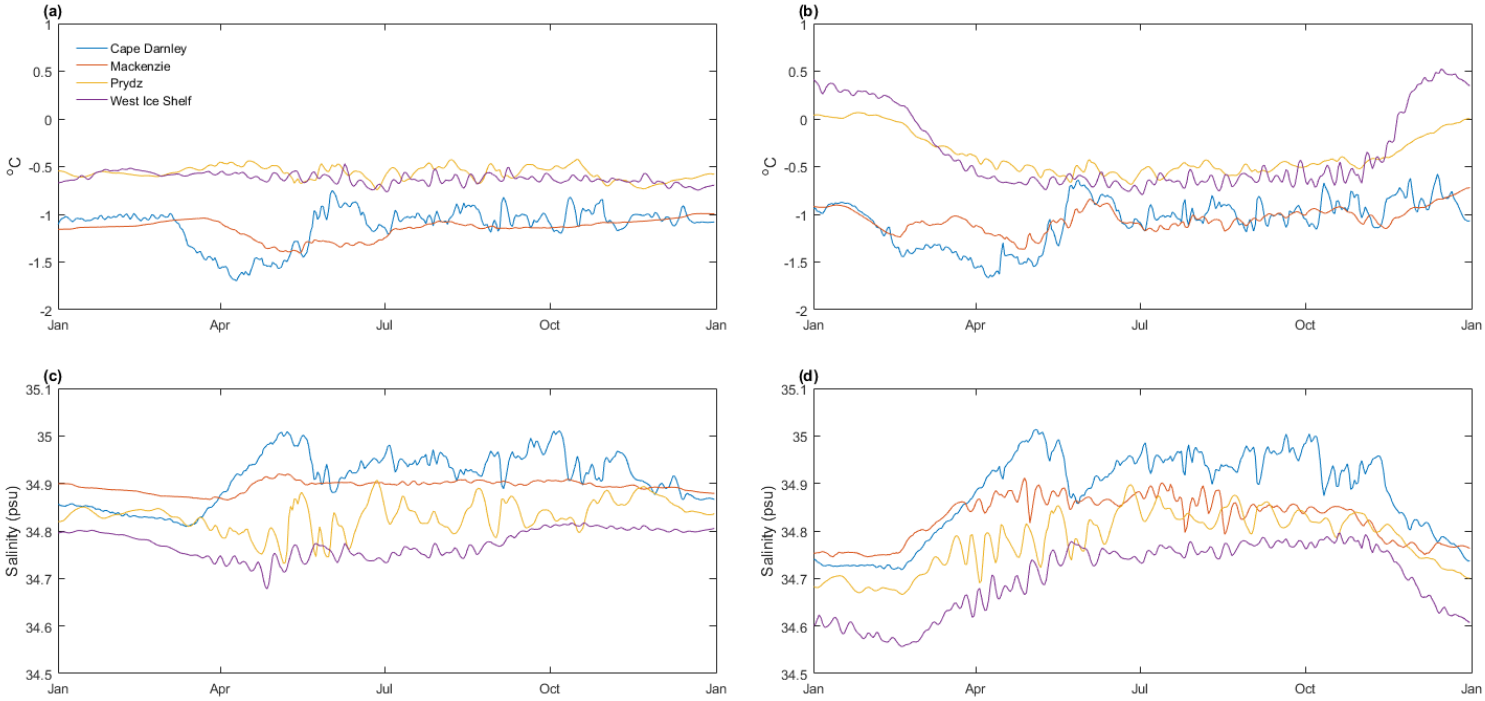


Fig 2. Annual temperature (a) and (c) and salinity (b) and (d) time series from ROMS.
Temperature and salinity averaged over the centroid for each of the four polynyas, for approximately the lower 50m (LHS) and top 50m (RHS) of the water column, respectively. Bathymetry was extracted from ROMS where depth is spread across 31 layers; the 50m threshold was selected based on which layers most closely represented the range. Legend for colours as shown in panel (a).

The ROMS time-series revealed unique signatures for each polynya (Fig 2 and S1 Appendix), but with similarities evident between the western (*i.e.* Cape Darnley and Mackenzie), and eastern (*i.e.* Prydz Bay and West Ice Shelf) two. Prydz Bay polynya and West Ice Shelf polynya were generally both warmer and fresher. While the seasonal and regional patterns were relatively well represented, in fact the ROMS representation of temperatures rarely approached the absolute freezing point of seawater (~ -1.85°C) in the western polynyas and not at all for the two easternmost polynyas; possibly in compensation of this the salinities were extremely high (e.g. commonly above 34.8 *psu*, Fig 2c and d).

1.2 T-S plots

As expected, the *in situ* seal observations (Fig 3a, c, e and g) were noisier than the ROMS output, which tended to occupy a smaller region of T-S space (Fig 3b, d, f and h). In general, the ROMS generated characteristics were more saline, by as much as 0.5 – 1 *psu*. ROMS represented most waters as sufficiently dense to be AABW precursor within all polynyas, and

as such a realistic evaluation of water mass formation was not possible. Despite this bias, there was good similarity in overall trends displayed between observed and modelled characteristics. For example, the water column structure at Cape Darnley from both observations and model output showed cooling throughout the season (panels a and b, light to dark blue), collapsing into a cold and highly saline water mass. For the other three polynyas, the seal observations throughout the autumn-winter were cold and saline while the ROMS representation was somewhat warmer.

1.3 Transects

The virtual transects provided a spatial summary of ocean conditions and seal distribution within and around the four Prydz Bay polynyas (Fig 4 and time-series animations in S2-S5 Videos). The polynya centres were clearly apparent as areas of cold, saline water. There was some evidence of a downslope flow of cold, salty water from both Mackenzie and Cape Darnley polynyas, with potential off-shelf flow also in the vicinity of West Ice shelf polynya. The northern section of the transects approaching and crossing the shelf break, were dominated by warmer, fresher water. This lens overlaid the polynya water particularly in the vicinity north of Mackenzie, which represents the deepest and most southerly polynya.

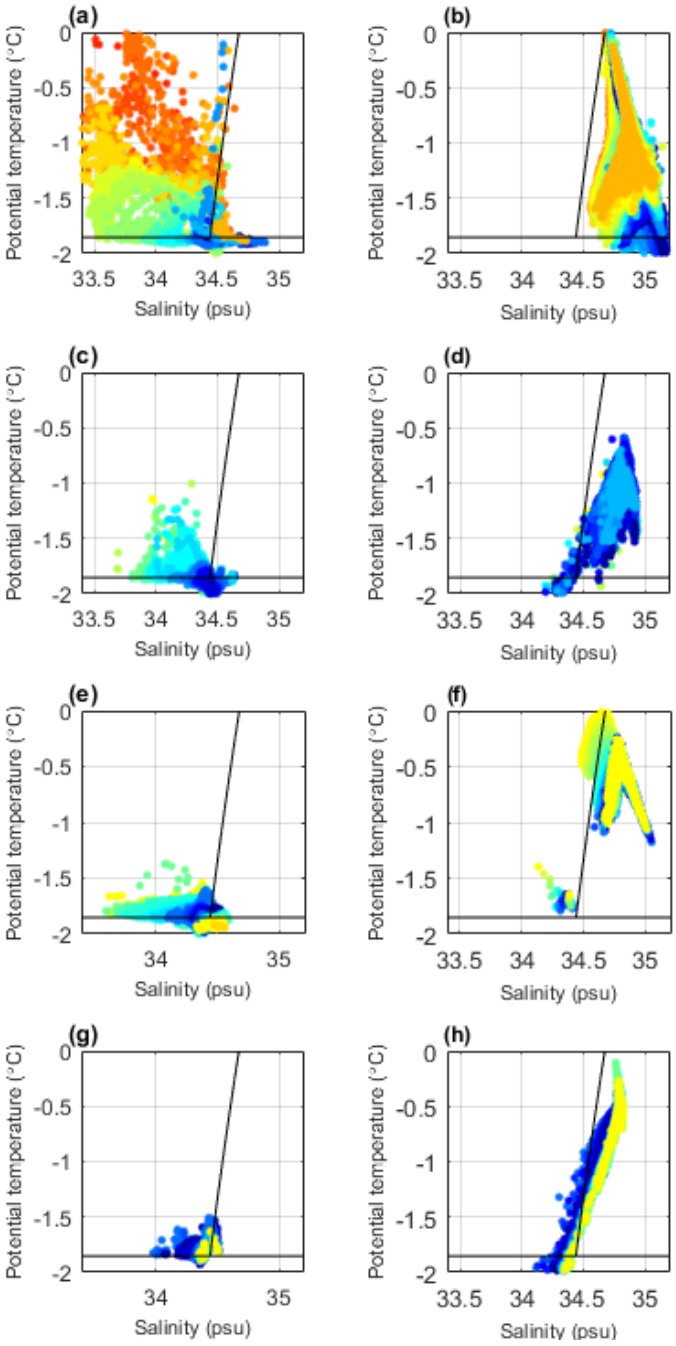


Fig 3. Comparative T-S plots between SES CTD (LHS) and ROMS (RHS) profiles within four East Antarctic polynyas.

a,b) Cape Darnley, c,d) Mackenzie Bay, e,f) Prydz Bay and g,h) West Ice Shelf. Profiles are coloured by season, where summer is deep red leading into dark blue during the middle of winter. Seal data include all observations at all depths extracted from within a surface heat flux contour defining the most active region of each polynya. The ROMS output displays a profile from every grid cell within the centroid, at fortnightly intervals. The approximate freezing point of water (-1.85°C) and the potential density curve representing AABW (σ_2=37.16) are shown in black.

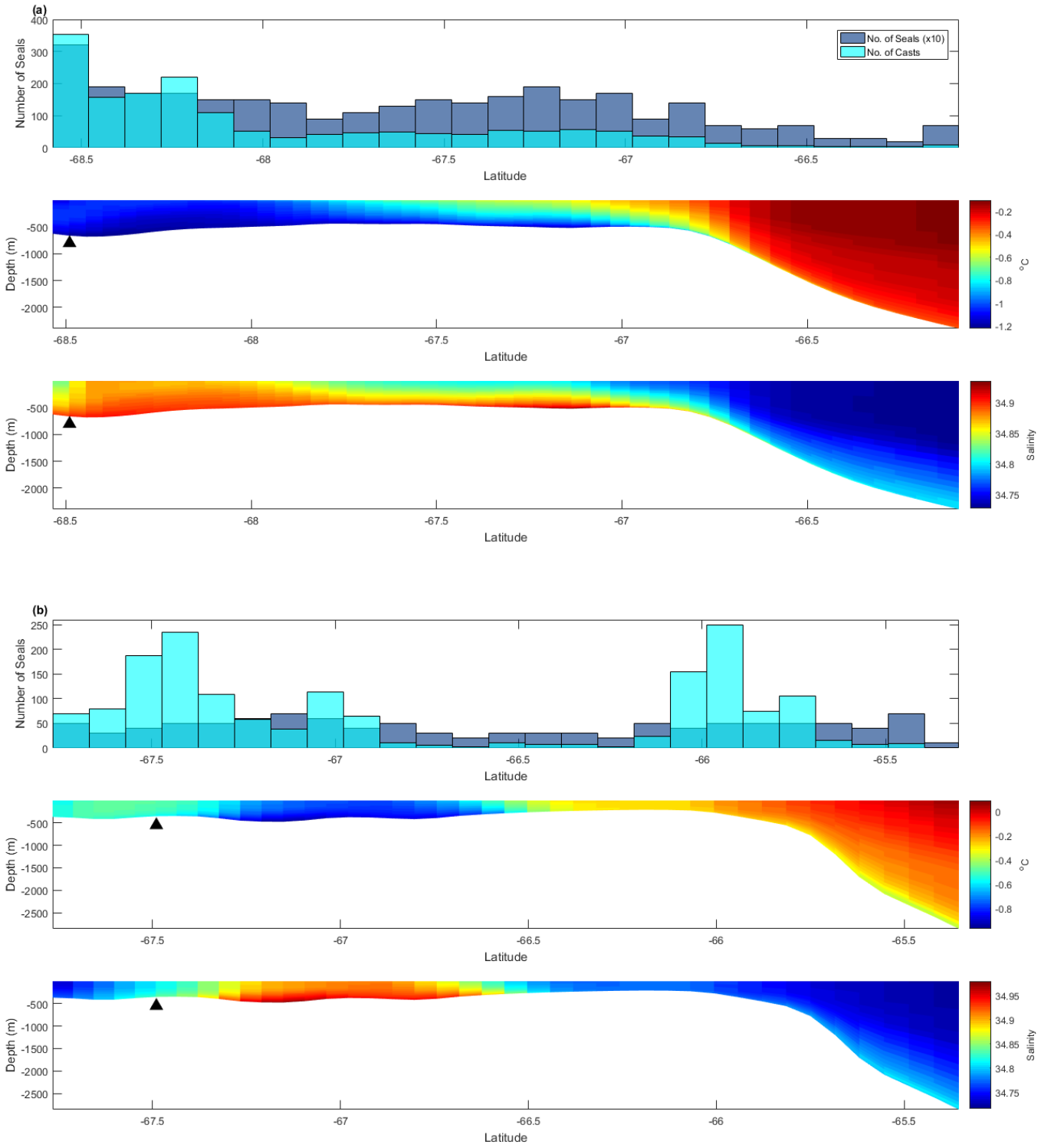


Fig 4. Virtual transects showing ROMS temperature and salinity in relation to the number of observed seals and seal CTD casts.

Virtual transects ran north-south from polynya centres to the shelf break. Modelled temperature and salinity was averaged over the freezing period (March – October). Transects represent a) Mackenzie Bay and b) Prydz Bay polynyas. The other two polynya transects are available in S1 Appendix, Fig. S1.2. The number of seals (top panel) was multiplied by a factor (x10) for clarity. Centroid location is represented by a black triangle.

For the Prydz Bay and West Ice Shelf polynyas, there was a concentration of seal observations close to the Antarctic continent, and highest seal numbers within the most active core areas (*e.g.* the cold, saline pocket around 67°S, Fig 4b). Along the Prydz Bay transect there was a second area of seal activity in a depression (~ 66°S) at the shelf break. The Cape Darnley transect also showed the greatest number of observations and seals not within the polynya core but closer to the shelf break (~ 66.9°S, S1 Appendix). Cape Darnley represents the shallowest polynya, with the majority of the shelf area being very cold and saline. For Mackenzie (Fig 4a) there was a high number of seals around both 68.5°S and 67°S, although the greatest number of observations were directly adjacent to the Amery Ice Shelf.

Overall, the virtual moorings, T-S and transect information taken together indicated that the ROMS output for the polynyas was adequately reproducing seasonal water column trends. Furthermore, the differences between modelled polynyas were sufficiently represented to suggest that the model was satisfactorily capturing distinct regional behaviours.

2. Characterisation of SES habitat use

2.1 Residence time results

The spatially gridded time-spent data revealed habitat usage patterns strongly centred on polynyas (Fig 5). The annual summary clearly showed that of all the available foraging locations the greatest time was spent in the region of the four polynyas (Fig 5a). Although visited by a high number of individual seals (Table 2) the Cape Darnley polynya had less concentrated use (~8 hours maximum per grid cell) compared to the other 3 polynyas (~20 hours). Also apparent was a concentrated usage of the shelf break area north of the Prydz Bay polynya, as previously identified within the virtual transect.

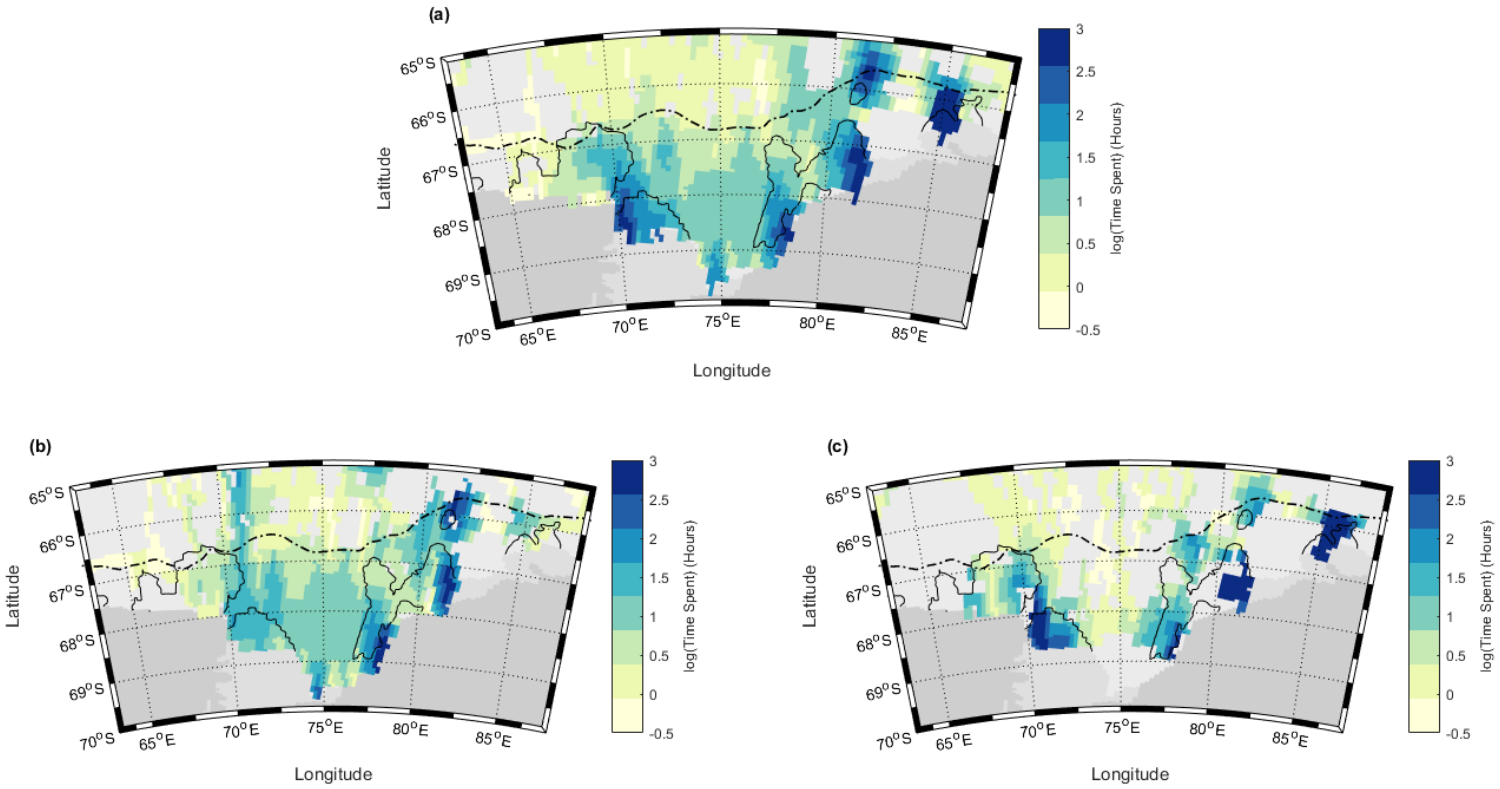


Fig 5. Maps showing the mean time spent per ROMS grid cell across all southern elephant seal individuals.

Residence time represented a) annually and during b) Post-Moult season 1 (February to April) and c) Post-Moult season 2 (May to July). Greater Polynya regions are outlined with the -40 W m^{-2} heat flux threshold (black) and the 1500m isobath (dotted line) indicates the shelf break.

During Post-moult 1 (*n* = 29936 KF locations), the Prydz Bay polynya and the shelf break area to the north (also indicated as a potentially active area by the -40 W m^{-2} contour) had the highest residence time. There was also evidence of a north-south transit route into the region, from a relatively concentrated usage observed along a route into Mackenzie Bay polynyas near 71°E. For PM1 there was generally high usage across the entire shelf as compared with off-shelf, indicating that the entire area was largely accessible at this time. Though there was less data available during early winter (PM2, *n* = 10349), the spatial usage patterns showed a stronger contraction towards the polynya areas during sea-ice advance; West Ice Shelf, Prydz Bay and Mackenzie polynyas were all regions of concentrated time spent during PM2. While the concentration of seals in Cape Darnley was lower there was still evidence of increased use in this polynya relative to the surrounding region.

2.2 Predictor fields

Due to the similarities between the predictor fields from each of the two seasons considered, only the fields for PM1 are shown (Fig 6). The predictor fields for PM2 are available in S3 Appendix.

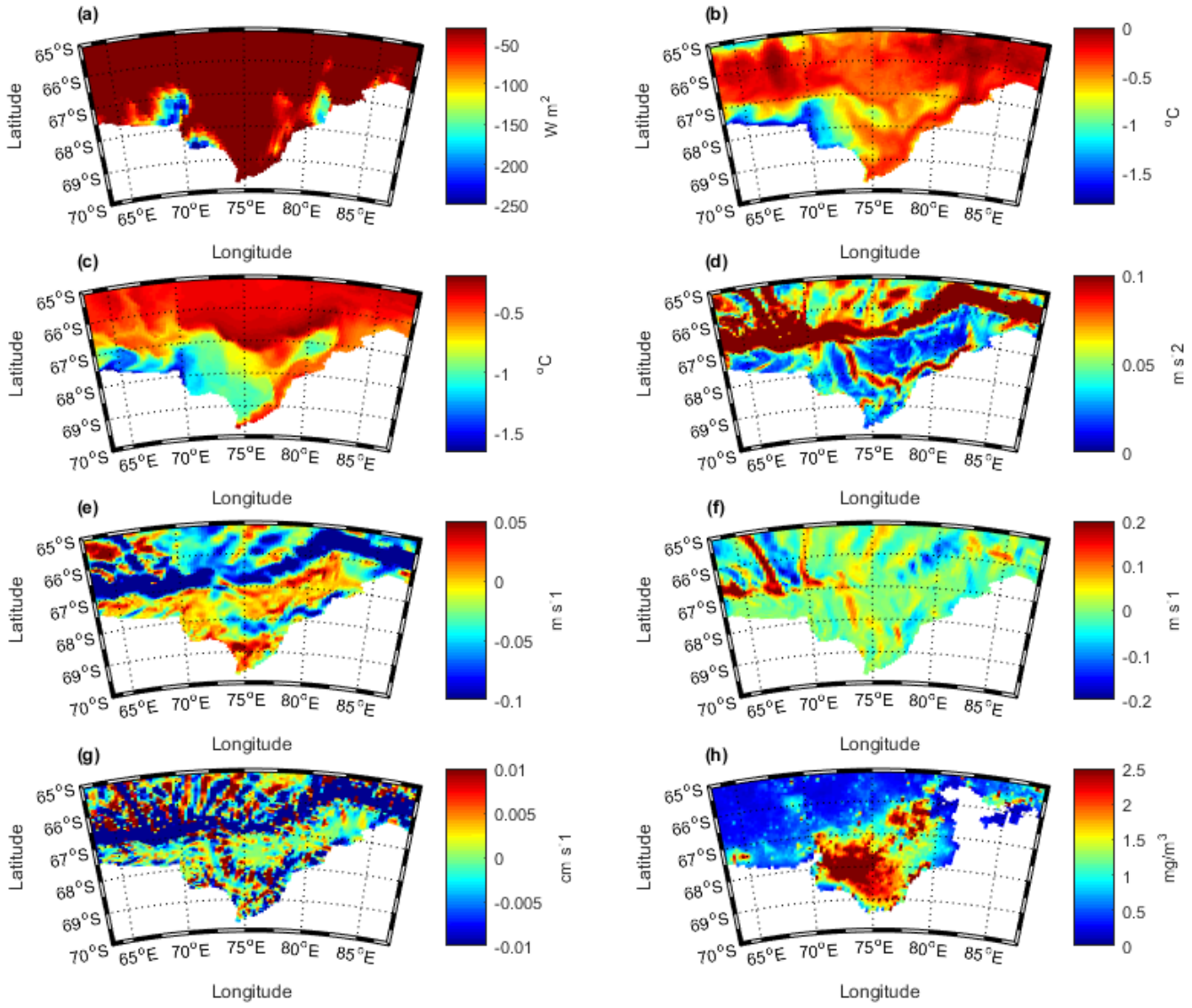


Fig 6. Physical and biological predictors fields used to build the seasonal GAMM for PM1.
a) Polynya location, surface heat flux (W m-^{2}) averaged over the freezing period (March to October); b) surface temperature (°C); c) bottom temperature (°C); and the d) total magnitude (m s^{-2}), e) eastward (m s^{-1}) (U), f) northward (m s^{-1}) (V), and g) vertical (cm s^{-1}) (W) components of bottom velocity; and h) surface Chlorophyll (mg/m^3) averaged over the previous season (November to January). Not shown is the 9th predictor field, bathymetry.

ROMS surface temperature for PM1 showed Cape Darnley and Mackenzie polynyas as distinctly colder than the surrounding region (Fig 6b). Bottom temperature additionally

highlighted the cold core of Prydz Bay polynya. A warm on-shelf flow originating in the north-east of Prydz Bay near 84°E, and flowing westward was evident in the bottom temperature as well as the bottom velocity and eastward (U) velocity fields, revealing the cyclonic circulation in the middle of the bay. Additionally, there was evidence of a strong westward jet along the shelf break representing the Antarctic Slope Current. When examining northward velocity (V), off-shelf flows of cold water originating from Cape Darnley were evident. Surface Chl-*a* for the preceding spring season (*i.e.* November – January) showed highest concentrations in the middle of Prydz Bay, with elevated levels evident within Prydz Bay and Mackenzie polynyas.

2.3 Model predictions

The goodness-of-fit statistics available for the full GAMs indicated a good fit from the final models, particularly given the complex spatial ecological data (PM1: adjusted R^2 = 0.484, deviance explained = 49.2%; PM2: adjusted R^2 = 0.589, deviance explained = 59.6%) and GAMMs (PM1: adjusted R^2 = 0.415; PM2: adjusted R^2 = 0.538). The predictor variables reported as significant for the final PM1 and PM2 GAMMs are given in Table 3. PM1 had three similarly influential predictors: bathymetry (AIC = 4540.483, R-sq. = 0.284), Chl-*a* (AIC = 4969.957, R-sq. = 0.188) and bottom temperature (AIC = 5001.159, R-sq. = 0.181) (these cited values relate to single predictor models, see S3 Appendix). The U and W bottom velocities were not retained in the final GAMM for PM1, and surface temperature and U bottom velocity were not retained for PM2. The influence of bathymetry is clear in the generally increased time spent across the entire shelf region (Fig 7a); partial residual plots (S3 Appendix) revealed a preference for shelf depths (200 – 700 m), with lower residence time offshore. Bottom temperature, associated with surface heat flux (or polynya location), influenced the concentrated polynya usage, especially evident within the Mackenzie and Prydz Bay polynyas. Increased residence time was associated with higher surface heat flux, and this predictor became more influential in PM2 (Fig S3.3 and S3.5, S3 Appendix). Increasingly concentrated polynya usage was predicted for all four polynyas during PM2 relative to PM1 (Fig 7b).

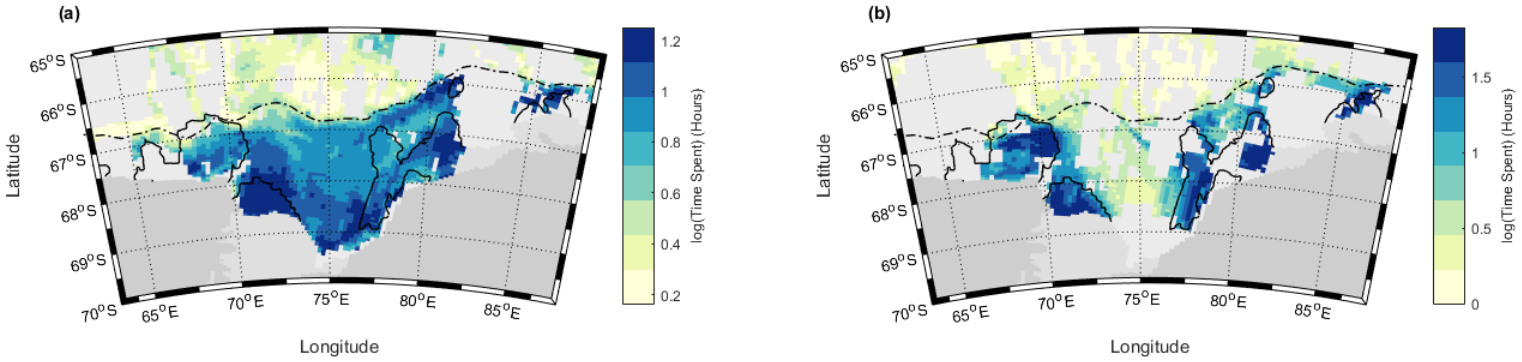


Fig 7. Generalised additive mixed model predictions of SES habitat selection.

For (a) Post-Moult 1 (PM1) and (b) Post-Moult 2 (PM2). Grid cell resolution of 0.25°. For PM1, surface heat flux (W m-^{2}), surface temperature (°C), bottom temperature (°C), magnitude (m s^{-2}) and northward (m s^{-1}) velocities, log transformed bathymetry (m) and log transformed Chl-*a* (mg/m^{3}) were considered. For PM2, surface heat flux (W m-^{2}), bottom temperature (°C), magnitude (m s^{-2}), vertical (cm s^{-1}) and northward (m s^{-1}) velocities, log transformed bathymetry (m) and log transformed Chl-*a* (mg/m^{3}) were considered.

PM2 was similar to PM1, with heat flux followed in influence by bathymetry and chlorophyll (Table S3.4, S3 Appendix). In both seasons, the magnitude of currents also played an important role: habitat usage increased with lower levels of water movement, spending relatively less time in the vicinity of higher flows along the shelf-break. Higher rates of downward vertical velocity along the shelf-break were weakly linked to an increase in predicted time spent (Fig S3.4 and S3.5) for PM2.

The available historical fish data (Fig 8) had patchy spatial coverage, with trawls inside polynyas only occurring at Cape Darnley and around the boundary regions for the other three. Consequently, this dataset was only used to qualitatively examine spatial patterns. The greatest proxy fish biomass occurred around the shelf break and within the centre of the bay, with high biomass also apparent in the vicinity of the warm shelf inflow near 84°E. Trawls within the Cape Darnley polynya revealed a relatively abundant number of species as did one trawl immediately adjacent to the Amery ice shelf.

Table 3. Statistical results from GAMMs fitted for (a) PM1 and (b) PM2.

(a)

	edf	F	p value
s(heat)	4.690	15.456	<0.001 (***)
s(s_temp)	5.590	8.079	<0.001 (***)
s(b_temp)	5.070	5.295	<0.001 (***)
s(vel)	3.115	22.143	<0.001 (***)
s(V)	1.000	30.421	<0.001 (***)
s(log.bath)	8.661	35.041	<0.001 (***)
s(log.Chlo)	6.629	13.353	<0.001 (***)

R-sq. (adj) = 0.415

Scale est. = 0.12378 n = 3408

(b)

	edf	F	p value
s(heat)	8.593	52.031	<0.001 (***)
s(b_temp)	8.433	15.618	<0.001 (***)
s(vel)	6.313	4.380	<0.001 (***)
s(V)	1.000	21.124	<0.001 (***)
s(log.bath)	7.347	27.868	<0.001 (***)
s(log.Chlo)	4.208	10.060	<0.001 (***)
s(W)	1.873	5.291	<0.01 (**)

R-sq. (adj) = 0.538

Scale est. = 0.22007 n = 2448

Heat = net surface heat flux average over the freezing period (March – October); used to represent polynya location; all other were variables seasonally averaged: s_temp = surface temperature, b_temp = bottom temperature, vel = bottom velocity magnitude; V = northward and W = vertical components of bottom velocity; log.bath = log transformed bathymetry, log.Chlo = log transformed surface chlorophyll (data from the previous season). edf represents estimated degrees of freedom.

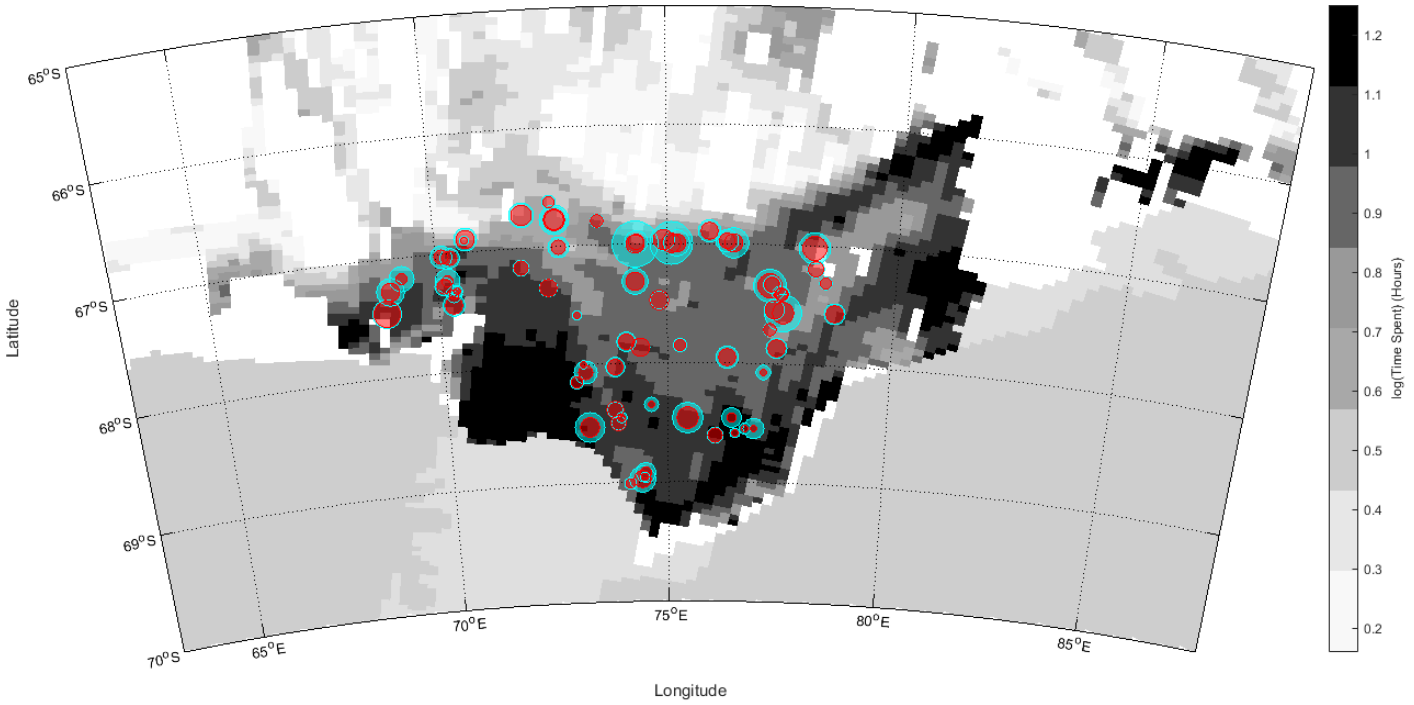


Fig 8. Historical pelagic and benthic fish data distribution.

Species richness (red) and proxy fish biomass (cyan) were obtained from total summed fish length standardized by trawl time (see Methods). Background shows predicted habitat selection for PM1.

Discussion

Southern elephant seals, a major Southern Ocean predator, are known to consistently target the Antarctic continental shelf and slope [e.g. 17, 19, 22] where they locate high-quality prey patches [23]. This study is the first to specifically focus on Antarctic shelf polynyas as important foraging locations. Characterising this key foraging habitat is not only ecologically important for our understanding of species responses to specific environmental conditions; the process also informs a more integrated understanding of these under-sampled regions. The physical importance of Antarctic coastal polynyas has been previously described [e.g. 1, 18], and this study provides important new insights into the bio-physical properties structuring these as predator foraging habitat. This study clearly showed seals spending greater time on-shelf within the Prydz Bay vicinity in East Antarctica, and exhibiting concentrated residence times within the four coastal polynyas in the region. Statistical analyses relating a suite of bio-physical predictors showed an influence of bathymetry, Chl-*a*, surface heat flux, bottom temperature and velocity on seal residence time. This provides the first description of polynya characteristics as a foraging habitat. Hypotheses are developed

regarding bio-physical and pelagic-benthic coupling in the vicinity of coastal polynyas, which lead to favourable conditions in terms of resources for predators.

The model evaluation process demonstrated that ROMS adequately represented the ocean properties and circulation in the study region for the purposes of this study. The ROMS output provided oceanographic context that supported two spatially correlated GAMMs with good fit to observed seal residence time enabling realistic predictions of habitat usage based upon bio-physical predictors.

1. Evaluation of ocean model output

1.1 Reproduction of main oceanographic features

Cape Darnley was the coldest and saltiest of the polynyas throughout all seasons, most likely a product of high rates of ice formation. Cape Darnley has been identified as having the second highest rate of ice production around Antarctica, behind the Ross Sea [1]. It is an important regional source of Antarctic Bottom Water (AABW), a cold dense water mass that is a major contributor to global overturning circulation [3, 5]. AABW originates as Dense Shelf Water (DSW) formed through brine rejection during sea-ice production [2-4]. The formation of DSW begins in March, at the start of the freezing period [5]. ROMS (with the imposed surface heat and salt fluxes) was able to produce such a trend with an increase in salinity and a drop in temperature throughout the water column at the start of March. Additionally, downslope flows of DSW in a north-west direction from Cape Darnley during the freezing period have been described [5]. The ROMS bottom velocity components (U and V) showed some evidence of this outflow.

The Prydz Bay and West Ice Shelf polynyas exhibited warmer and less saline trends than either Cape Darnley or Mackenzie. A large cyclonic gyre centred in the Amery Depression has been associated with a coastal current that circulates warm Modified Circumpolar Deep Water (MCDW) into the Bay and across the calving front of Amery Ice Shelf [13] and continues westward [42]. This gyre is responsible for the circulation of warm Modified Circumpolar Deep Water (MCDW) The various ROMS velocity components represented this flow, and the ROMS temperature time series for the Prydz Bay and West Ice Shelf polynyas reflected the influence of this warmer water.

The potential influence of the gyre and other circulation features such as eddies [43] may explain the weekly cycles in the T-S time series apparent within both Prydz Bay and Mackenzie polynyas (Fig 2 and S1 Text). Additionally, the small T-S phase space occupied

by the Mackenzie Bay polynya could be attributed to the accumulation of High Salinity Shelf Water (HSSW) due to the outflows from the Amery Ice Shelf. This cold, saline water mass, along with the isolation of Mackenzie due to surrounding bathymetry [18], may have contributed to the model simulating intensely cold, highly saline water throughout the year.

1.2 Model limitations

When comparing ROMS output to SES CTD profiles, a definite saline bias was evident in the modelled output. One likely cause is resolution of the model. The circumpolar domain of the model meant that the horizontal grid resolution was configured at 0.25°. This is at the coarse end of a 'high' resolution regional model and it is possible this was not adequate for simulating the fine scale processes within the region. In particular the model struggled to represent water properties as the column approached the freezing point, overcompensating regarding salinity [13, 44].

Improvements may be obtained via a finer-scale ocean model configured to the specific study region, enabling tuning to better represent specific local processes [13, 44]. The ROMS implementation was also climatological; a more direct comparison with the observational dataset would be possible from an inter-annual ROMS implementation (e.g. with forcing that coincides with the SES data, *i.e.* 2007 – 2015). Future developments may explore a fully-coupled sea-ice component in the model (as opposed to prescribed heat and salt fluxes) to reproduce the evolution of water masses and allow an investigation of finer scale processes; and/or a bio-geochemical sub-model [e.g. 45].

Despite the saline bias found within the ocean model output, for the purposes of this study spatial dynamics and seasonal trends were considered priority in evaluating the model's performance. Similarly, the absolute values of salinity and temperature were less important than a correct representation of differences between polynyas and seasonal differences within each polynya.

1.3 Elephant seal habitat use: observed and predicted

Examining elephant seal tracking data, combined with ocean model output to provide regional context, revealed new insights into factors influencing habitat usage within Prydz Bay. Overall, the observed and modelled habitat usage showed high residence times in the four coastal polynyas relative to the surrounding region. The most concentrated occupancy occurred within the Mackenzie and Prydz Bay polynyas, increasingly so as the season progressed to early winter.

Interestingly, the Cape Darnley polynya was visited by a relatively high number of individuals but they spent less time overall in this polynya compared to the Mackenzie and Prydz Bay polynyas. Models relating bio-physical characteristics of polynyas with the seal time spent per grid predicted suitable foraging location, with concentrated seal usage especially during PM2 (May – July) in the Cape Darnley polynya. Thus this polynya had presumably (*i.e.* based on models) favourable bio-physical conditions for seal foraging activity despite the lower observed time-spent compared to the Mackenzie and Prydz Bay polynyas. Tagging location may have played some role in the observed lower rates of residency; for those individuals tagged at Davis Station (n=42) Cape Darnley is certainly available/accessible (in terms of travel distance) but may be less optimal than the more proximate options of Mackenzie and Prydz Bay. It has also been identified that the relationship between foraging behaviour and oceanographic conditions may change with the scale investigated [19]; the scale used in this study may have been too coarse to detect fine-scale environmental conditions targeted by seals within the region. An investigation into these finer-scale variables in future studies may better reveal why the Cape Darnley polynya had a lower average residency time.

Foraging of SES around Antarctica has been described in deep oceanic waters [22] around the Antarctic shelf break [17] and in shelf waters. Within the greater Prydz Bay region, this study revealed the significance of bathymetry as a physical predictor for both seasonal GAMMs, describing a predominant depth for SES habitat usage between ~200 – 700 m. While this study did not examine open ocean foraging, those seals that migrate to this area clearly focus their time in the shelf and shelf-break vicinities, supporting the concept that the shelf region generally represents favourable foraging habitat [19, 22, 23]. Within this region, coastal polynyas have been described as key oceanographic features [1, 5, 18]; the importance of surface heat flux (a proxy for polynya area) as a predictor of habitat usage implicated polynyas as ecologically important regions for SES during both PM1 (February – April) and PM2 (May – July).

Residence time during PM2 showed concentrated polynya use and a reduced usage of other available shelf habitat. SES are influenced by the extent of sea-ice [46], and the majority of Prydz Bay is ice-covered during PM2. Concentrated polynya use during this season may have been due to habitat contraction because of ice formation and subsequent breathing constraints; however, the persistence of polynya usage during the previous season (PM1) suggested that there may be foraging benefits for polynya fidelity even when sea ice is absent. The potential negative influence of colder waters on the mobility of prey such as fish

631 and squid [19, 47] is a phenomenon that may be at play in the cold bottom waters of
632 polynyas. Polynyas support high phytoplankton blooms compared to surrounding ice-
633 covered waters in early spring and have been described as site of concentrated biological
634 activity supporting rich ecosystems throughout the year [7, 48]. Primary productivity (surface
635 Chl-*a*) was represented within each seasonal predictive model as an average of the previous
636 season to support the development of secondary production. The significance of this
637 predictor, as well as surface heat flux and bathymetry, suggested that polynya location and
638 biological production were together important factors determining relative rates of habitat
639 usage within the Prydz Bay region, especially leading into winter.
640 In the Commonwealth Bay polynya it has been hypothesised that towards the end of
641 summer, surface productivity is convected through the water column [49] leading to a sub-
642 surface Chl-*a* maximum that supports secondary productivity (zooplankton, small fish etc.)
643 used by seals later in the season. The influence of Chl-*a* within both statistical models was
644 likely due to this relationship between high rates of primary productivity during early spring
645 and summer and the effect this has on secondary production within polynyas. Vertical ROMS
646 velocities (W) revealed sinking water specifically within Prydz Bay polynya and Mackenzie
647 polynya. This vertical movement, which may have entrained primary production down
648 through the water column, was significant in describing habitat use during PM2. A higher
649 resolution ocean model could enable an investigation of these fine-scale water movement
650 features to verify this transfer of biomass.
651 Notably, diving behaviour of SES on the Antarctic is thought to be predominantly
652 benthic (e.g. >75% of dives) [19, 20]. This study therefore proposes an expansion to the
653 above hypothesis [49], whereby the bio-physical coupling from surface to subsurface
654 productivity is likely to extend throughout the water column as it becomes fully convected
655 later in the season to promote pelagic-benthic coupling, a linkage between the surface pelagic
656 system and the benthos. Recent work has highlighted the diversity of benthic community
657 assemblages that are strongly influenced by bathymetry and other water characteristics,
658 including distance to polynyas [24]. Through enhanced vertical carbon flux, polynyas may
659 support rich benthic communities [50]. A productive benthic community could represent a
660 relatively stable and known forage opportunity for migratory predators, in comparison to
661 seasonally transient pelagic production in oceanic waters.
662 Historical fish data suggested a greater number of species and increased biomass
663 around regions of warm in-flow, and within the Cape Darnley polynya. However, the dataset
664 provided poor spatial coverage and there was little information for the Mackenzie, West Ice

shelf and Prydz Bay polynyas. The lack of data meant that fish distribution was not included as a biological predictor within the developed GAMMs. The age and scarcity of this dataset highlighted the need for updated pelagic and benthic fish sampling within Prydz Bay region in order to better biologically describe prey availability for SES and other marine predators.

Conclusion

The results of this study suggest that the most important foraging locations within Prydz Bay region are polynyas, particularly the Cape Darnley, Mackenzie and Prydz Bay polynyas. These polynyas vary in their levels of activity, are impacted by the central gyre within the region and correspond to areas of cold water outflows and warm water inflows, respectively. Future vessel-based survey work targeting the question of whether benthic communities and associated fish assemblages are more productive inside or outside of these areas would provide valuable insights into the true nature of the proposed pelagic-benthic coupling. Obtaining prey field data at relevant spatio-temporal scales is expensive but necessary to enable a better biological understanding of how prime foraging habitat is structured, and provide a pathway into characterising the region as habitat for other marine predators such as other seals, penguins and flying seabirds.

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